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The effects of ecology and evolution on avian flight morphology

Natalie Wright

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Natalie A. Wright

Candidate

Biology

Department

This dissertation is approved, and it is acceptable in quality and form for publication:

Approved by the Dissertation Committee:

Christopher C. Witt, Chairperson

Jeffery Long

Blair Wolf

James Brown

**THE EFFECTS OF ECOLOGY AND EVOLUTION ON AVIAN
FLIGHT MORPHOLOGY**

by

NATALIE A. WRIGHT

B.S., Zoology, University of Florida, 2005
M.S., Zoology, University of Florida, 2009

DISSERTATION

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Doctor of Philosophy

Biology

The University of New Mexico
Albuquerque, New Mexico

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Dedication

This dissertation is dedicated to Bob Dickerman, whose enthusiastic contributions to ornithology will continue to influence and aid many new generations of biologists. He collected a great many of the specimens used in this manuscript. Without his generous support of the Museum of Southwestern Biology ornithology collection, this dissertation would not have been possible. He is greatly missed and remembered fondly.

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Ph.D., Biology, University of New Mexico

ABSTRACT

The tendency for flying organisms to possess small genomes has been interpreted as evidence of natural selection acting on the physical size of the genome. Nonetheless, the flight-genome link and its mechanistic basis have yet to be well established by comparative studies within a volant clade. Is there a particular functional aspect of flight such as brisk metabolism, lift production, or maneuverability that impinges on the physical genome? I measured genome sizes, wing dimensions, and heart, flight muscle, and body masses from a phylogenetically diverse set of bird species. In phylogenetically controlled analyses, I found that genome size was negatively correlated with relative flight muscle size and heart index (i.e., ratio of heart to body mass) but positively correlated with body mass and wing loading. The proportional masses of the flight muscles and heart were the most important parameters explaining variation in genome

size in multivariate models. Hence, the metabolic intensity of powered flight appears to have driven genome size reduction in birds.

Birds evolving on islands have been the subject of thousands of scientific studies. These studies have revealed a tendency for island populations to adapt to a generalist niche. I found consistent shifts in shape, but not body size, following island colonization. Island-restricted volant species evolved smaller flight muscles than their continental relatives, with the degree of reduction greatest on islands of low species diversity. The decrease in flight muscle size was accompanied by an increase in leg length, reflecting a shift in investment from forelimbs to hindlimbs. Evolution along the trajectory toward flightlessness occurred in island bird populations from all nine families studied.

I tested how reduced flight muscles and longer legs affect take-off performance in birds on the small, depauperate island of Tobago. I found that birds on Tobago had slower maximum velocity and maximum acceleration during take-off relative to conspecifics on the larger island of Trinidad. Initiation of wingbeats occurred later during take-off in populations on the island of Tobago in two species. Across all individuals, birds with smaller flight muscles initiated wingbeats later and achieved peak acceleration earlier during take-off. Lower predation pressures on small, species-poor islands likely permit the slower take-off velocities that result from island birds' reduced flight muscles. These predictable evolutionary changes in the avian *bauplan* may explain why volant island birds are particularly vulnerable to introduced predators.

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Chapter 1: Metabolic ‘engines’ of flight drive genome size reduction in bird

Abstract

The tendency for flying organisms to possess small genomes has been interpreted as evidence of natural selection acting on the physical size of the genome. Nonetheless, the flight-genome link and its mechanistic basis have yet to be well established by comparative studies within a volant clade. Is there a particular functional aspect of flight such as brisk metabolism, lift production, or maneuverability that impinges on the physical genome? We measured genome sizes, wing dimensions, and heart, flight muscle, and body masses from a phylogenetically diverse set of bird species. In phylogenetically controlled analyses, we found that genome size was negatively correlated with relative flight muscle size and heart index (i.e., ratio of heart to body mass) but positively correlated with body mass and wing loading. The proportional masses of the flight muscles and heart were the most important parameters explaining variation in genome size in multivariate models. Hence, the metabolic intensity of powered flight appears to have driven genome size reduction in birds.

Introduction

Genome size evolution

The causes and consequences of variability in nuclear genome size have been a subject of research and discussion for many decades (e.g., Mirsky and Ris 1951; Thomas 1971), but much remains to be learned. Several intriguing comparative patterns have been identified that provide insights into the evolutionary forces that have shaped genome size diversity. As a notable example, a proposed link between powered flight and reduced

genome sizes in bats, birds, and pterosaurs has been interpreted as evidence that the metabolic demands of flight exerted selective pressures for small cells with reduced DNA content (Hughes and Hughes 1995; Organ and Shedlock 2009; Zhang and Edwards 2012). These three historical instances of flight origins and genome constriction are suggestive, but comprise meager statistical evidence for a mechanistic link. Furthermore, ancestral state estimates for the archosaur phylogeny revealed that much of the genome size reduction in the ancestors of modern birds predated the origin of flight (Organ et al. 2007).

If flight ability imposes strong evolutionary constraints on genome size, then interspecific diversity in flight ability should explain at least some of the variability in genome size within volant clades. Indeed, evidence to this effect has begun to accumulate, with some caveats. Hughes and Hughes (Hughes and Hughes 1995) found that flightless birds have larger genomes than volant relatives, but this pattern became non-significant after accounting for phylogenetic inertia (Organ and Shedlock 2009). Hovering hummingbirds exhibit the highest mass-specific metabolic rates among vertebrates (Suarez 1992), and a large sample of hummingbird species was found to have uniformly small genomes and to include the smallest amniote genome measured to date (Gregory et al. 2009). In 74 species of temperate, migratory passerine birds, genome size was positively associated with wing-loading index, indicating that species that have evolved larger wings for flight efficiency have also evolved smaller genomes (Andrews et al. 2009). Additional components of flight performance beyond wing size and shape have yet to be investigated for potential effects on genome size.

The metabolic rate hypothesis is the leading explanation for reduced genomes in volant organisms (Hughes and Hughes 1995). According to this hypothesis, the size of the genome imposes a minimum size constraint on nucleated cells, and the higher proportional surface areas of smaller cells make them conducive to higher metabolic flux (Gregory 2001). The energy required to produce lift and thrust requires sustained high metabolic output (Ward et al. 2002), resulting in indirect selection for smaller genomes to reduce the size that nucleated cells are required to be (Gregory 2001). In keeping with this hypothesis, genome size and red blood cell size are negatively correlated with resting metabolic rate across vertebrates and within vertebrate classes, including birds (Gregory 2002). Aside from the putative metabolic rate effect, a reduction of cellular DNA content and a concomitant decrease in cell size might allow flying organisms to achieve a reduction in body mass (Gregory 2002) and may even enhance efficiency of neural function associated with maneuverability (Gregory 2002; Andrews and Gregory 2009). Under the latter mechanisms, wing loading and wing shape would be predicted to correlate strongly with genome size.

The avian flight 'engines'

The pectoral and cardiac muscles are the metabolic 'engines' of avian flight and therefore might illuminate the causes of genome size evolution. The avian pectoral flight muscles, comprising the pectoralis major and supracoracoideus, provide the power for downstroke and upstroke, respectively. The pectoral flight muscles vary greatly in size across birds, ranging from ~5% of the body mass in rails and ground cuckoos to over 30% in some hummingbirds and pigeons (Hartman 1961; 2014). The ratio of heart mass to body mass, the heart index (Vinogradov and Anatskaya 2006), indicates the relative

allocation of resources for oxidative metabolism. Both maximum cardiac output and aerobic power input scale with heart mass to a power of ~ 0.88 (Bishop and Butler 1995; Bishop 1997), and heart mass accurately predicts maximum metabolic rate and aerobic scope (Bishop 1999). Although the flight muscles and heart generate and supply power for a substantial portion of locomotory and thermogenic activity (Hohtola 1982; Hohtola and Stevens 1986; Chappell et al. 1999; Swanson et al. 2013), species variation in relative flight muscle size and heart index indicates the degree of importance of burst power (Tobalske et al. 2003) and endurance flight performance (Bishop 1997), respectively. Previous studies using non-phylogenetic methods have found that genome size was negatively correlated with heart index in birds ($n=53$), mammals, non-avian reptiles, and amphibians (Vinogradov and Anatskaya 2006).

This study

The link between flight and reduced genome size has received substantial attention (e.g., Hughes and Hughes 1995; Gregory 2002; Altshuler et al. 2004; Organ and Shedlock 2009; Zhang and Edwards 2012), but there is not yet a broad comparative analysis of variation in the flight and metabolic structures as they relate to genome size within a volant clade. In this study, we developed the largest internally consistent dataset on bird genome sizes, comprised of 18 orders, 76 families, and 422 species. Species were selected to represent a diversity of environments, ecological niches, and life histories. We sought to elucidate the effects of flight on genome size evolution during the diversification of birds using measurements of three flight-related structures: the heart, the flight muscles, and the wings.

Materials and methods

Data collection

We captured wild birds and drew blood from the brachial vein to prepare blood smear slides. Birds were euthanized, prepared as museum specimens with frozen tissues, and deposited at the Museum of Southwestern Biology (University of New Mexico, USA) and/or Centro de Ornithología y Biodiversidad (Lima, Peru). Slides of blood blotted from the liver were prepared for individuals from which we were unable to draw blood. One investigator (N.A.W.) estimated genome size by Feulgen image analysis densitometry using the protocol of Hardie et al. (Hardie et al. 2002), with chicken, *Gallus gallus* (1.25pg), as the standard, and >200 nuclei measured per individual. For species represented by more than one individual, mean within-species standard deviation of genome size estimates was 0.035, while the among-species standard deviation in genome size was 0.138. The low intraspecific variation, relative to interspecific variation, suggests that estimates of genome size using only one individual should be sufficiently representative of the species. Genome size estimates are available in Supplementary Materials Table S1.

We weighed each bird and extracted and weighed whole hearts (after blotting to remove blood) and the pectoralis major and supracoracoideus flight muscles. Relative flight muscle size was calculated by dividing total flight muscle mass by body mass. Heart index was calculated by dividing the heart mass by the body mass (Vinogradov and Anatskaya 2006). We used proxies for aspect ratio and wing-loading that could be measured from museum study skins. The hand-wing index, or Kipp's index (Kipp 1959; Claramunt et al. 2012), is equal to the distance between the tip of the longest primary and

the tip of the first secondary divided by the wing chord (Claramunt et al. 2012); larger values indicate more pointed wings. This can be calculated as $(WL-SL)/WL$, where WL is the wing chord and SL is the distance from the wrist joint to the tip of the first secondary (Claramunt et al. 2012). This index is correlated with dispersal ability in interspecific comparisons (e.g., Burney and Brumfield 2009; Dawideit et al. 2009; Claramunt et al. 2012). WL is comprised of the lengths of the manus and the longest primary feather, both of which are strongly correlated with overall wing length and scale isometrically with other wing components such as the ulna (Nudds 2007; Nudds et al. 2011; Wang et al. 2011). Bird wings are generally shaped as one-quarter of an oval. Thus wing area was estimated as the area of an oval divided by four ($WL*SL*\pi/4$). Wing area estimates were used to approximate wing loading (body mass/total wing area).

Species averages for the above morphological measurements were obtained from specimens at the Museum of Southwestern Biology and Florida Museum of Natural History. We were unable to obtain all morphological measurements for all species. Thus, with genome size estimates for 422 species, we analyzed two overlapping datasets of species-average values: (A) relative flight muscle size, heart index, and body mass for 289 species; and (B) relative flight muscle size, heart index, body mass, hand-wing index, and wing-loading for 193 species.

Data analysis

We used a time-calibrated phylogeny based on published DNA sequences for over 6,000 species of birds (Burleigh et al.) that we trimmed to include only the species in our genome size dataset. We placed the ~5% of the species in our dataset that were not represented in this tree following the methods of Sibly et al. (Sibly et al. 2012). We used

this tree to calculate phylogenetic independent contrasts, test for phylogenetic signal in the data, and perform phylogenetic generalized least squares (PGLS) models under a Brownian motion model in R version 2.15.1 (R Core Team 2012) using packages APE (Paradis et al. 2004), caper (Orme et al. 2012), and nlme (Pinheiro et al. 2012). We log-transformed body mass prior to analyses. We used AIC to select the best model(s) for non-phylogenetic linear regression and PGLS. Multi-parameter models were discarded from consideration if a nested model, containing a subset of the same parameters, had a better AIC score (Burnham and Anderson 2002; Arnold 2010).

We tested for constraints on maximum genome size that might be associated with high flight ability (i.e., high values of relative heart mass, relative flight muscle size, and hand-wing index, or low values of body mass and wing loading). For each measure of flight ability, we binned values into 15 equally spaced bins, following (Derryberry et al. 2012). We selected the species with the maximum genome size value in each bin to include in the upper-bound set. We then tested whether these upper-bound values of genome size decline with increasing flight ability more dramatically than do all other values. To do this, we used ANCOVA to test for the significance of an interaction term between the measure of flight ability and whether a sample was included in the upper-bound set.

Results

There was significant phylogenetic inertia in genome size across the entire 422-species dataset. Pagel's lambda was 0.88 (95% C.I.: 0.788-0.943), indicating that phylogenetic nonindependence should be accounted for in comparative analyses.

Blomberg's K , which estimates the amount of phylogenetic signal in the data relative to the amount expected for a trait evolving along the same tree by Brownian motion (Blomberg et al. 2003; Garland et al. 2005), was 0.451 (significantly greater than zero, $p = 0.001$).

Body mass was negatively correlated with heart index (PGLS: $df = 286$, $p < 0.001$, $R^2 = 0.043$), but not with relative flight muscle size (PGLS: $df = 286$, $p = 0.13$, $R^2 < 0.01$). Heart mass scaled with body mass to a power of 0.78 in our dataset (95% CI: 0.75, 0.81).

In single variable phylogenetic models, genome size was negatively correlated with heart index and relative flight muscle size and positively correlated with body mass and wing loading (Figures 1, 2; Table S2). In the larger dataset (289 species), the top ranking PGLS models (i.e., those within 95% cumulative AIC weight after excluding models with uninformative parameters) included heart index and relative flight muscle size as significant predictors of genome size (Table 1). In the reduced dataset (193 species), the top ranking PGLS models included relative flight muscle size, wing loading, heart index, and body mass as important predictors of genome size; wing loading was unique among these variables in that it was not statistically significant ($p < 0.05$) in any of the top models (Tables 2, 3).

We found evidence of constraints on genome size with respect to some measures of flight ability. The slopes of regressions of genome size by heart index and hand-wing index, respectively, were more steeply negative for upper-bound points than for other points (Table 4; Figure 2), indicating that large genome sizes were particularly unlikely to occur in species with large hearts or pointed wings.

Visualization of the evolution of genome size across the avian tree revealed lability among families and orders (Figure 3). Orders differed significantly from one another in average genome size (ANOVA: $p < 0.001$, $df = 404$; Figure 3; Table S3), with Apodiformes exhibiting the smallest average genome sizes. Of the orders represented by at least 5 species, Piciformes had the largest and most variable genomes (Figures 2, 3, Table S3). Passerine genomes were significantly smaller than those of non-passerine orders [t-test: $p = 0.006$; $df = 180$; 95% CI of mean difference: (-0.08, -0.013)]. Deep phylogenetic structure in genome size was evident among major clades of passerines. Nine-primaried oscines had larger genomes, on average, than other passerines [t-test: $p < 0.001$; $df = 128$; 95% CI of mean difference: (0.019, 0.071)]. However, extreme values were not necessarily consistent with these broader patterns. For example, out of all passerine families, the smallest average genome sizes were found in two oscine families, the vangas (Dicruridae; C-value 1.13 pg) and the indigobirds and whydahs (Viduidae; C-value 1.14 pg); and the largest passerine genome was not found in a nine-primaried oscine, but rather the phainopepla (*Phainopepla nitens*; C-value 1.83 pg).

Discussion

Which aspects of flight are related to genome size?

Flight muscle size, heart size, body size, wing aspect ratio, and wing loading reveal different aspects of flight ability in birds. Each of these parameters, with the exception of wing aspect ratio, is individually correlated with genome size across a wide swath of the avian tree (Figures 1, 2; Table S2), strongly supporting the idea that small genomes and overall flight ability are linked. In multivariate models, flight muscle size,

heart size, body size, and wing loading explain unique fractions of genome size variation, with flight muscle size and heart size being the most consistently important predictors of genome size. There was no indication that wing aspect ratio (measured by hand-wing index) explains any additional variation. These findings are consistent with the hypothesis that the cellular metabolic rate during flight, rather than constraints on aerial maneuverability or lift, was the main cause of genome size reduction in birds.

Relative flight muscle size was the single best predictor of genome size: it was significant in almost all top models in both the 289- and 193-species datasets (Tables 1, 2, 3). Flight muscles provide the power for flapping flight, and as such are most important in strong take-offs and bursts of speed in flight, where power requirements are highest (Tobalske et al. 2003). Thus, large flight muscles are expected to indicate an evolutionary response to selection for rapid take-off ability or powered acceleration during flapping flight. Additionally, the size of the flight muscles is a primary determinant of exercise-induced maximum metabolic rate or thermogenic capacity in intra-specific comparisons for at least five species of birds that have been tested, representing three orders and a wide range of body sizes (Hohtola 1982; Hohtola and Stevens 1986; Chappell et al. 1999; Hammond et al. 2000; Swanson et al. 2013).

Heart index was an important and statistically significant predictor of genome size in top PGLS models (Tables 1, 2, 3). The size of the heart constrains its stroke volume and, as a result, limits maximum cardiac output, aerobic power, exercise-induced maximum metabolic rate, and aerobic scope (Bishop and Butler 1995; Bishop 1997, 1999). Routine powered flight incurs a 10-20 fold sustained increase in metabolic rate

(Ward et al. 2002). Therefore, heart index in birds should closely reflect aerobic power requirements for sustained flight.

Body mass generally shows strong phylogenetic signal (Blomberg et al. 2003) and correspondingly was present and significant in all top ranking non-phylogenetic models, but not all PGLS ones (Tables 1-3). Either body mass or heart index was significant (or nearly so) in every top ranking model, but in no model were both parameters significant (Tables 1, 2). Heart mass scales with body mass to a power of 0.78 in our dataset, very close to the three-quarter power scaling of metabolic rate (West et al. 1997). Heart size may be a more precise predictor of metabolic rate than body mass because it is more directly, mechanistically connected to metabolism than is body mass, in part because it scales isometrically with cardiac stroke volume (Grubb 1983; Bishop and Butler 1995). Indeed, heart mass has been shown to explain variation in exercise-induced maximum metabolic rate after accounting for the effects of body mass (Bishop 1999). Consistent with this, for our largest dataset, AIC decisively indicated that heart index was the best single predictor of genome size and that body mass did not explain residual variation after heart index was included in the model (Table 1).

Hand-wing index did not appear in top ranking PGLS models (Tables 2, 3). The link between genome size and hand-wing index in conventional regression (Figure 2; Tables 3, S2) appears to have been driven by phylogenetic inertia, specifically the confluence of extreme values in the hummingbirds and swifts (Apodiformes). Accordingly, the effect of hand-wing index disappears when covariance due to phylogeny is taken into account. Long, pointed wings improve high-speed flight performance by reducing drag, especially at higher speeds (Videler 2005). High aspect ratio is typical of

bird species that are long-distance migrants or aerial foragers (Lockwood et al. 1998; Saino et al. 2010). However, some birds with high aspect ratios engage in flight styles with low energetic demand (e.g., dynamic soarers) and accordingly would not achieve the metabolic intensity associated with flapping flight.

Wing loading was included as an important predictor variable in several top PGLS models, but was never a significant variable in these models ($p > 0.25$; Tables 2, 3). Birds with low wing loading are able to produce lift with low metabolic energy input (Rayner 1988). The tendency for aerial specialists to have low wing loading is thought to be the basis for the previous finding that passerines with low wing loading tend to have small genomes (Andrews and Gregory 2009). However, wing-loading reflects a balance of ecological and biomechanical pressures and many strong, energetic flyers have high wing loading (e.g., pigeons, doves, and many ducks (Rayner 1988)). Thus, wing loading, like aspect ratio, is at least partly decoupled from flight metabolism and is unlikely to explain genome size variation if the maximum sustained rate of cellular metabolism is the key driver of genome size reduction.

The importance of accounting for phylogenetic inertia

Genome size exhibited phylogenetic signal across the avian tree, as indicated by Pagel's lambda and Blomberg's K values that were significantly greater than zero. Related taxa were less similar in genome size than expected under a model of evolution by Brownian motion, as indicated by the Blomberg's K value being less than one (Blomberg et al. 2003; Garland et al. 2005). This apparent lability is more typical of behavioural traits than constrained life history traits such as body mass (Blomberg et al. 2003) and it suggests that divergent selection has acted on genome size, although

measurement error is also expected to contribute to this effect. Nonetheless, as a result of the pervasive phylogenetic inertia in genome size, the PGLS analyses are expected to be more informative regarding potential mechanisms in cases where they differ from non-phylogenetically controlled analyses (Rohlf 2006). Hence, in the 289-species analysis, the inclusion of body mass and exclusion of heart index in top ranking non-phylogenetic model are likely examples of Type I and Type II errors, respectively (Table 1).

Constraints on genome size associated with extreme flight ability

Genome size appears to be constrained with respect to heart index and hand-wing index, as indicated by the different slope of the regression for upper bound points (Figure 2, Table 4). Species with small hearts or rounded wings may have either large or small genomes, but strong flyers with large hearts or pointed wings appear to be constrained to have small genomes. This pattern suggests that genome size evolves neutrally in poor flyers, but that large genomes impose a fitness cost on birds that experience high metabolic intensity during flight.

Genome size variation across the tree of birds

The hummingbirds have exceptionally small genomes with low variation in genome size (Gregory et al. 2009). This study is the first to show that the nearest relatives of hummingbirds, the swifts (Apodidae), also have small genomes (Figure 3, Table S3). Like many other traits of hummingbirds that are thought to be adaptive for metabolically intensive flight (e.g. high aspect ratio, reduced hindlimbs, large pectoral flight muscles), reduced genome size likely evolved in the common ancestor of hummingbirds and swifts (Figure 3).

The Pici clade, comprised of the woodpeckers, honeyguides, barbets, and toucans, exhibits exceptionally large genomes, while members of its sister taxon, the Galbulae (Galbulidae and Bucconidae), have fairly small genomes (Figure 3, Table S3). Members of the clade including Piciformes and Coraciiformes are anomalously variable, with sister lineages sometimes differing substantially in genome size (Figure 3, Tables S1, S2). For example, the two honeyguide species included in this study, both in the genus *Indicator*, exhibit strikingly different genome sizes (1.38 pg vs. 2.05 pg; Table S1). Han et al. (Han et al. 2011) found large numbers of transposable elements in the Piciformes-Coraciiformes clade, which may contribute to the large average genome sizes and the high degree of variation observed in the group (Kidwell 2002; Organ and Shedlock 2009). The macromutations that may have caused fluctuations in genome size among Piciformes deserve investigation by comparison of genome sequences. To this end, frozen tissues are archived for all of our voucher specimens (Table S1).

Conclusions

The long recognized link between flight and small genome size has been decisively confirmed using interspecific comparisons within the most diverse volant group. Four flight-related characteristics show that the evolution of enhanced flight ability tends to be accompanied by genome size reduction. In comparisons among phylogenetically corrected models, the best predictors of genome size proved to be the sizes of the flight muscles and heart, rather than the size or shape of the wings. The avian flight muscles generate cellular metabolic energy in proportion to their enormous bulk (5-30% of total body mass), providing the majority of power output for aerial locomotion and

thermogenesis. Cardiac output constrains the power input for cellular metabolism and is in turn limited by heart size. Consistent with the metabolic rate hypothesis, these two components of the metabolic flight ‘engine’ implicate the rate of energy use as a key driver of repeated evolutionary reductions in avian genome size.

Table 1: Models predicting genome size within 95% cumulative AIC weight after excluding models with uninformative parameters for the 289-species dataset (f = relative flight muscle size; h = heart index; m = body mass). PGLS = phylogenetic generalized linear model; regression = conventional (non-phylogenetically corrected) linear regression.

model type	model	adj. R^2	df	p-values	AIC	AIC weight
PGLS	f + h	0.073	286	f: 0.0038; h: 0.0043	-557.31	0.91
PGLS	h	0.049	287	h < 0.001	-522.19	0.07
regression	f + m	0.38	286	f < 0.001; m < 0.001	-486.49	0.999

Table 2: Models predicting genome size within 95% cumulative AIC weight after excluding models with uninformative parameters for the reduced dataset (N = 193 species; f = relative flight muscle size; h = heart index; wl = wing-loading; hw = hand-wing index; m = mass). PGLS = phylogenetic generalized linear model; regression = conventional (non-phylogenetically corrected) linear regression.

model type	model	adj. R ²	df	p-values	AIC	AIC weight
PGLS	f + h + m + wl	0.12	188	f < 0.001; h: 0.49; m: 0.006; wl: 0.26	-369.18	0.46
PGLS	f + h + wl	0.088	189	f: 0.005; h: 0.057; wl: 0.40	-368.03	0.26
PGLS	f + m + wl	0.12	189	f < 0.001; m: 0.001; wl: 0.26	-366.75	0.13
PGLS	f + h + m	0.119	189	f < 0.001; h: 0.49; m: 0.007	-364.52	0.04
PGLS	f + h	0.09	190	f: 0.006; h: 0.019	-364.41	0.04
PGLS	h + wl	0.054	190	h: 0.001; wl: 0.66	-363.06	0.02
regression	f + m + hw + wl	0.41	188	f < 0.001; m < 0.001; hw: 0.041; wl: 0.063	-346.44	0.52
regression	f + m + hw	0.40	189	f < 0.001; m < 0.001; hw: 0.033	-344.88	0.24

regression	f + m + wl	0.40	189	f < 0.001; m < 0.001; wl: 0.051	-344.14	0.17
regression	f + m	0.39	190	f: 0.002; m < 0.001	-342.24	0.06

Table 3: Cumulative model weights for each predictor variable in the five-parameter (N = 193 species) and three-parameter (N = 289 species) datasets, calculated by summing Akaike model weights for all models that included the variable of interest, following (Arnold 2010). PGLS = phylogenetic generalized linear model; regression = conventional (non-phylogenetically corrected) linear regression.

	<u>5-parameter (N = 193)</u>		<u>3-parameter (N = 289)</u>	
	PGLS	regression	PGLS	regression
relative flight muscle size	0.966	0.996	0.93	0.999
wing loading	0.894	0.691	NA	NA
heart index	0.834	0.302	0.99	0.27
body mass	0.657	0.999	0.06	0.999
hand-wing index	0.002	0.742	NA	NA

Table 4: Comparison of upper bound regressions to standard linear regressions for genome size by each flight ability predictor variable. We used an ANCOVA with an interaction term between the predictor variable and whether a sample was included in the upper-bound set.

predictor variable	95% CI for upper bound slope	95% CI for all points slope	two-tailed p-value for upper bound interaction
heart index	(-32.3, -19.1)	(-18.1, -12.1)	p = 0.018
relative flight muscle size	(-1.78, -0.07)	(-1.33, -0.70)	p = 0.78
body mass	(0.04, 0.21)	(0.15, 0.20)	p = 0.24
hand-wing index	(-0.0095, -0.0049)	(-0.0028, -0.00090)	p = 0.003
wing loading	(-10.26, 19.96)	(20.42, 33.71)	p = 0.86

Figure 1: Phylogenetic independent contrasts (PIC's) of species mean values for genome size plotted as a function of heart index, relative flight muscle size, body mass, hand-wing index, and wing-loading.

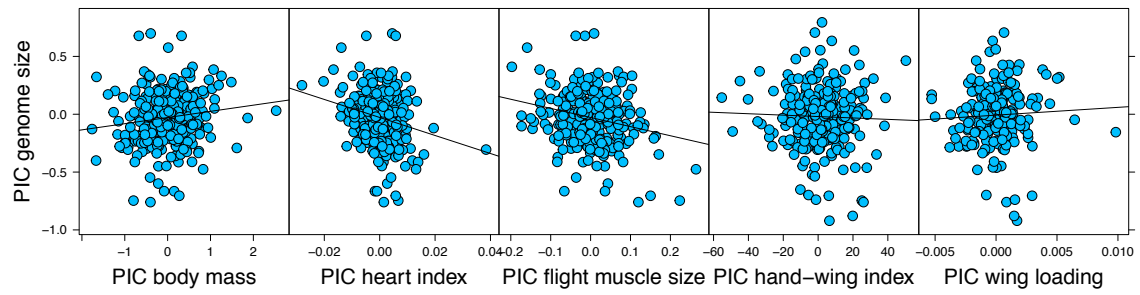


Figure 2: Species mean values for genome size plotted as a function of heart index, relative flight muscle size, wing loading, hand-wing index, and body mass, colour-coded by order. Solid lines are all-points regression lines; dashed lines are upper bound regression lines.

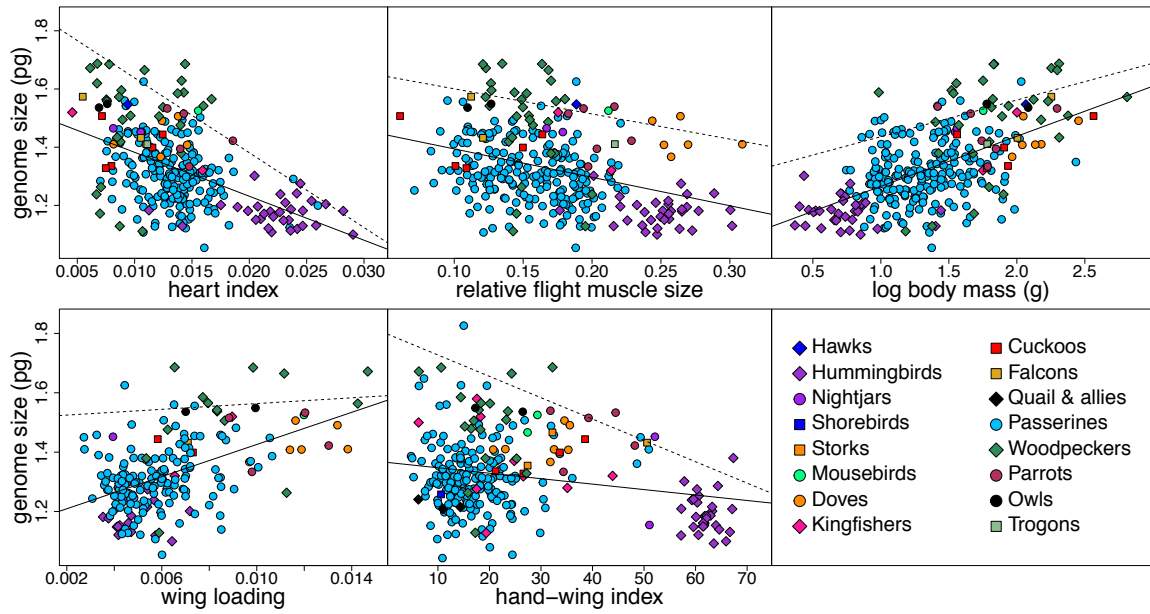
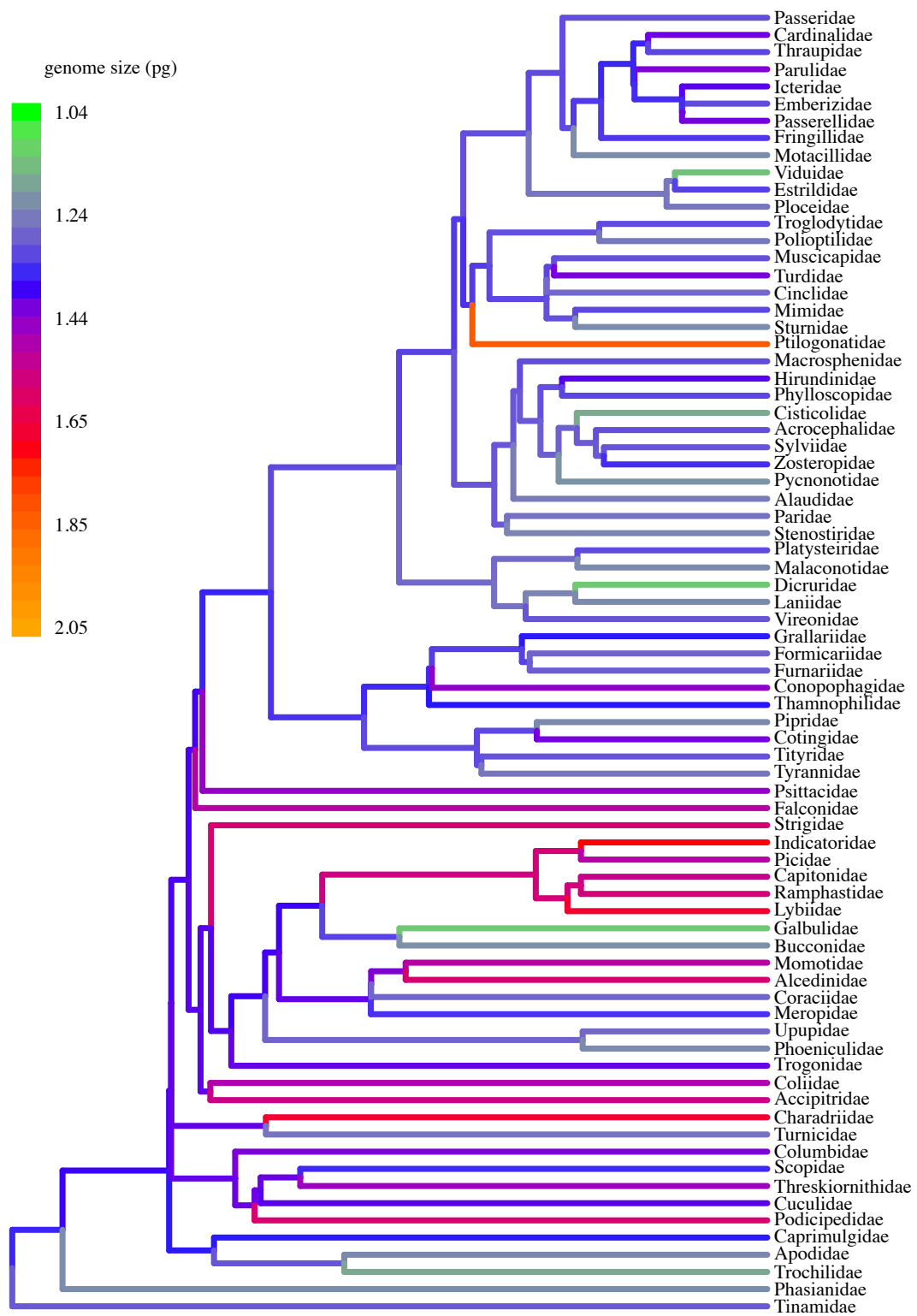


Figure 3: Family-level phylogeny with terminal branches colour-coded by the average genome size for each family. Internal branches are colour-coded by the estimated ancestral genome size, using maximum likelihood ancestral character state estimation in the R package APE (Paradis et al. 2004). The tree is from Jetz et al. (Jetz et al. 2012) and was downloaded from birdtree.org with data preference set to "Hackett all species."



Chapter 2: A new island rule for birds: Evolution toward flightlessness

Abstract

Birds evolving on islands have been the subject of thousands of scientific studies. These studies have revealed a tendency for island populations to adapt to a generalist niche. We found consistent shifts in shape, but not body size, following island colonization. Island-restricted volant species evolved smaller flight muscles than their continental relatives, with the degree of reduction greatest on islands of low species diversity. The decrease in flight muscle size was accompanied by an increase in leg length, reflecting a shift in investment from forelimbs to hindlimbs. Evolution along the trajectory toward flightlessness occurred in island bird populations from all nine families we studied. These predictable evolutionary changes in the avian *bauplan* may explain why volant island birds are particularly vulnerable to introduced predators.

Main Text

Birds on islands inspired the discovery of evolution and continue to illuminate its mechanisms (Darwin 1859; Wallace 1881). Numerous studies have argued that avian body size and bill size evolve toward a generalist niche in species-poor island communities (Grant 1965; Clegg and Owens 2002; Lomolino 2005; Boyer and Jetz 2010; McClain et al. 2013). In this vein, the ‘island rule’ holds that taxa converge towards intermediate body size after colonizing islands; but this ecogeographic rule-of-thumb has proven to be a poor predictor of evolutionary trends in real island populations (Meiri et al. 2006; Meiri et al. 2008; Meiri et al. 2011; Leisler and Winkler 2015). Rather than

changes in size, the most striking evolutionary transition among island birds has been the loss of flight, which has occurred over a thousand times in diverse lineages of rails, parrots, pigeons, owls, waterfowl, and songbirds (Slikas et al. 2002; Steadman 2006; Kirchman 2009). Each instance of the evolution of flightlessness involved a profound change in body shape due to reallocation of mass from the forelimbs to the hindlimbs (Steadman 2006; Steadman et al. 2013). It is not known whether the vast majority of island bird populations, which are volant, also exhibit predictable evolutionary trends in body shape.

Evolution of flightlessness is accompanied by near elimination of costly flight muscles, but this adaptive energy savings can only be realized in the absence of terrestrial predators (McNab 1994, 2002). Flightlessness has never evolved in continental landbird lineages smaller than ratites (Paleognathae) or terror birds (Phorusrhacidae). Whereas flightlessness evolves in response to the absence of terrestrial predation, we hypothesize that island species that retain flight may reduce their investment in the flight apparatus, inducing a qualitatively similar but more subtle shape change. Our previous work showed that five species of birds evolved smaller flight muscles and longer legs on the small island of Tobago (Wright and Steadman 2012). In this study we tested whether island size and species richness could predict shifts in the relative investment in forelimbs versus hindlimbs in 366 bird populations from 80 islands across the Pacific and Caribbean.

We weighed the two avian pectoral flight muscles, the pectoralis major and the supracoracoideus, from over 8,000 birds carcasses at the time of museum specimen preparation (Wright and Steadman 2012; Wright et al. 2014). These represented 868

landbird species, 38 of which are restricted to islands . With all taxa combined, island-restricted species had smaller flight muscles, relative to body mass, than their continental relatives (phylogenetic general linear model (PGLS): $p < 0.001$, df: 2 and 866).

We measured skeletal elements of museum specimens from island taxa in families Trochilidae, Columbidae, Alcedinidae, Zosteropidae, Rhipiduridae, Meliphagidae, Monarchidae, Pachycephalidae, and Thraupidae. We used the length of the sternal keel as an index of pectoral muscle mass . We expected flight muscle and hindlimb morphology to evolve in concert, because ontogenetic tradeoffs cause hindlimb and forelimb locomotor investment to be negatively correlated (Heers and Dial 2014). We focused on changes in the length of the tarsometatarsus, the distal-most long bone in the avian leg. In our dataset, keel length and tarsometatarsus length were negatively correlated across taxa (PGLS: $p < 0.001$, df: 2 and 364; Figs. S3-S10) and in intraspecific comparisons (e.g., *Coereba flaveola*: $p < 0.001$, adj. $R^2 = 0.34$, df: 1 and 237; table S1). We corrected for body size in all analyses using the first axis of a principal component analysis of morphometric variables .

We developed an index of hindlimb vs. forelimb investment from a principal component analysis of keel and tarsometatarsus lengths . This “air-ground index” represents larger flight muscles with shorter legs. We used island species richness and island area as metrics of insularity, because each is mechanistically related to and provides an index of ecological pressures that affect evolution, such as numbers of competitor and predator species (MacArthur and Wilson 1967; Steadman 2006), diversity of resources available (MacArthur and Wilson 1967), and population size (MacArthur and Wilson 1967). Our dataset included islands ranging from 786,000 km² with over 620

landbird species to 19 km² atolls supporting only 3 species of resident landbirds. We used PGLS across all taxa with island population as the unit of analysis to test whether locomotor morphology evolved predictably with island characteristics.

Air-ground index, representing larger flight muscles and shorter legs, was positively correlated with island landbird species richness and island area across 366 island populations in PGLS analyses (Table 5; Figure 4). Landbird species richness and island area also correlated positively with our air-ground index within families and genera in non-phylogenetic analyses (Figure 5; Tables S5, S7). This pattern was statistically significant at $p < 0.01$ for 14 out of 15 study taxa (Table S7). At the extreme, species richness explained 60% of the variation in air-ground index in *Todiramphus* kingfishers on Pacific islands. Analyses of keel size and leg length individually followed the same pattern (Tables 1, S6, S8), with keel length positively correlated with island species richness at $p < 0.001$ in 13 of 15 study taxa and tarsometatarsus length negatively correlated with species richness at $p \leq 0.01$ in 13 of 15 taxa (Table S8).

We tested whether island birds are evolving toward a generalist body size as they become more hindlimb-dominant. Most of our study taxa are small-bodied birds, with a median body mass of 14g, and maximum body mass of 915g. The island rule predicts that small taxa should become larger with greater insularity. In PGLS analysis across all taxa with island population as the unit of analysis and using PC1 as an estimate of body size, we found that body size was weakly negatively correlated with species richness and island area (Table 5). There was no consistent pattern, however, across lineages. Body size correlated negatively with species richness in five of 15 study taxa, and positively in another five taxa in non-phylogenetic analyses within genera and families (Tables S6 and

S8). We tested whether the relationship between body size and species richness within a genus correlated with mean body size of the genus. The island rule predicts a positive relationship, with larger taxa evolving smaller body sizes on islands of low species richness and small taxa becoming larger with insularity (Figure S1). We found no significant relationship between the magnitude or direction of body size changes on islands and mean body size (Figures S2-S4), either across all taxa ($p=0.65$, df: 1 and 17) or within taxa (Columbidae: $p=0.73$, df: 1 and 4; Passeriformes: $p=0.24$, df: 1 and 7).

These results indicate a previously undetected ecogeographic rule for birds, that island birds evolve reduced flight muscles and larger legs in response to the reduced ecological pressures associated with small, depauperate islands. We suggest that this be referred to as the ‘avian island rule’. The rule is supported by data from nine avian families and four orders that encompass huge variation in lifestyle, diet, foraging behavior, flight style, and body plan. Our findings are robust to analytic method, taxonomic scale, and island system. Even highly aerial taxa such as hummingbirds, fruit-doves, and flycatchers exhibit morphological trends towards flightlessness despite being unlikely to completely lose flight.

Island landbird species richness is a better predictor of flight muscle size and tarsometatarsus length than island area (Tables 1, S5-S7). While species richness and island size are correlated (in our island dataset: $p<0.001$, adj. $R^2=0.42$, df: 1 and 78) and mechanistically linked (MacArthur and Wilson 1967), the islands in this study vary in remoteness, archipelago size, geologic history, and topographic complexity. These size-independent factors affect the complexity of ecological communities, including landbird species richness (MacArthur and Wilson 1967; Steadman 2006; Franklin and Steadman

2008). Our results suggest that the reduced flight muscles and longer legs of island birds are mechanistically linked to depauperate ecological communities rather than the geophysical properties of small islands,.

The exact functional consequences of reduced flight muscles and longer legs have not been tested, but they likely result in slower maximal flight speeds and slower, more hindlimb-dominated take-offs (Earls 2000; Tobalske et al. 2003; Tobalske et al. 2004; Heers and Dial 2014). Because the avian flight muscles provide the power for flight, their size is important in times of greatest power requirements, which are at the highest and lowest airspeeds (Tobalske et al. 2003). Longer legs are associated with terrestriality and a greater variety of perch types (Grant 1965), but are also important in takeoff. Birds use a leg thrust to generate initial velocity during takeoff (Earls 2000; Tobalske et al. 2004), such that their wings and flight muscles do not have to generate lift at an airspeed of zero, where power requirements are especially high (Tobalske et al. 2003). Longer legs provide a longer lever, increasing the velocity and force generation during the leg thrust. They could therefore help compensate for the smaller flight muscles during take-off by increasing the initial velocity at which the wings and flight muscles must generate lift, thus decreasing takeoff power requirements for the flight muscles. It is becoming clear that there is a tradeoff between hindlimb and forelimb investment and performance across species, within individuals across ontogeny (Heers and Dial 2014), and within species across populations (this study).

Lower overall predation pressure on islands of low species richness might release birds from the need for large, powerful flight muscles for escape flights. Islands of lower species richness have lower diversity of competitors, predators, habitats, and food sources

(MacArthur and Wilson 1967; Raffaele et al. 1998; Steadman 2006). Many of the islands in this study have native raptor species, but no native mammalian predators. When only one or a few raptor species are present on an island, they tend to be generalists (Raffaele et al. 1998; Steadman 2006). Avian specialist predators tend to only occur on islands of high species richness and likely exert a higher predation pressure on landbirds for escape abilities than do generalist species. The lack of specialist predators on lower diversity islands would select for the reduction of flight muscle size and concomitant increase in hindlimb investment.

Longer legs may be selected for in island birds due to conditions that favor perch generality and greater time spent foraging on the ground. Birds on islands of low species richness tend to become more generalist in their foraging habits, often using a wider variety of habitats, food sources, and perch types (Grant 1965; Feinsinger and Swarm 1982; Keeler-Wolf 1986). Passerines often evolve longer legs on islands in association with using wider varieties of perch types (Grant 1965; Leisler and Winkler 2015). Additionally, longer legs in birds are associated with higher degrees of terrestriality. Selection for longer legs would drive a concomitant decrease in pectoral flight muscle investment (Heers and Dial 2014). Whether selection is acting primarily to reduce flight muscles or increase leg length, with the other change occurring due to ontogenetic tradeoffs, is unclear. Insularity may select directly for both smaller flight muscles and longer legs.

The vulnerability of volant island birds to introduced predators is sometimes attributed to “island tameness,” an evolved reduction in vigilance to predators (Lack 1983; Cooper et al. 2014). Our results suggest that volant island birds also have reduced

physical capacity for escape, exacerbating their vulnerability to humans, rats, cats, and snakes (Blackburn et al. 2004). Flight-related biomechanical and physiological mechanisms, such as reduced ability to escape via flight, may play a considerable role in volant island birds' extinction risks.

Table 5: Results from phylogenetic generalized linear model (PGLS) analyses of skeletal data for island population means. R^2 values are for the models after phylogenetic signal has been taken into account. Island species richness and island area were log-transformed before analysis. Keel and tarsometatarsus lengths are body size-corrected. Body size variable is the first principal component from a PCA of skeletal measurements.

dependent variable	predictor variable	coefficient	AIC	p-value	R^2	df
air-ground index	species richness	0.34	86	<0.001	0.45	364
air-ground index	area	0.09	128	<0.001	0.28	364
keel length	species richness	3.62	1908	<0.001	0.41	364
keel length	area	1.02	1938	<0.001	0.27	364
tarsometatarsus length	species richness	-1.13	1036	<0.001	0.32	364
tarsometatarsus length	area	-0.29	1073	<0.001	0.18	364
body size	species richness	-0.16	530	0.004	0.03	364
body size	area	-0.05	535	0.018	0.02	364

Figure 4: Avian populations on islands of low species richness have repeatedly evolved smaller flight muscles and longer legs (Tables 1, S2). Each pair of phylogenetic trees represents island population-level relationships within one of nine study families. Air-ground index is mapped onto the left tree in each pair and species richness is mapped onto the right. Darker and lighter gray represent greater and smaller values, respectively, of air-ground index and species richness. Greater air-ground index indicates larger flight muscles and shorter legs. Species richness is on a log scale.

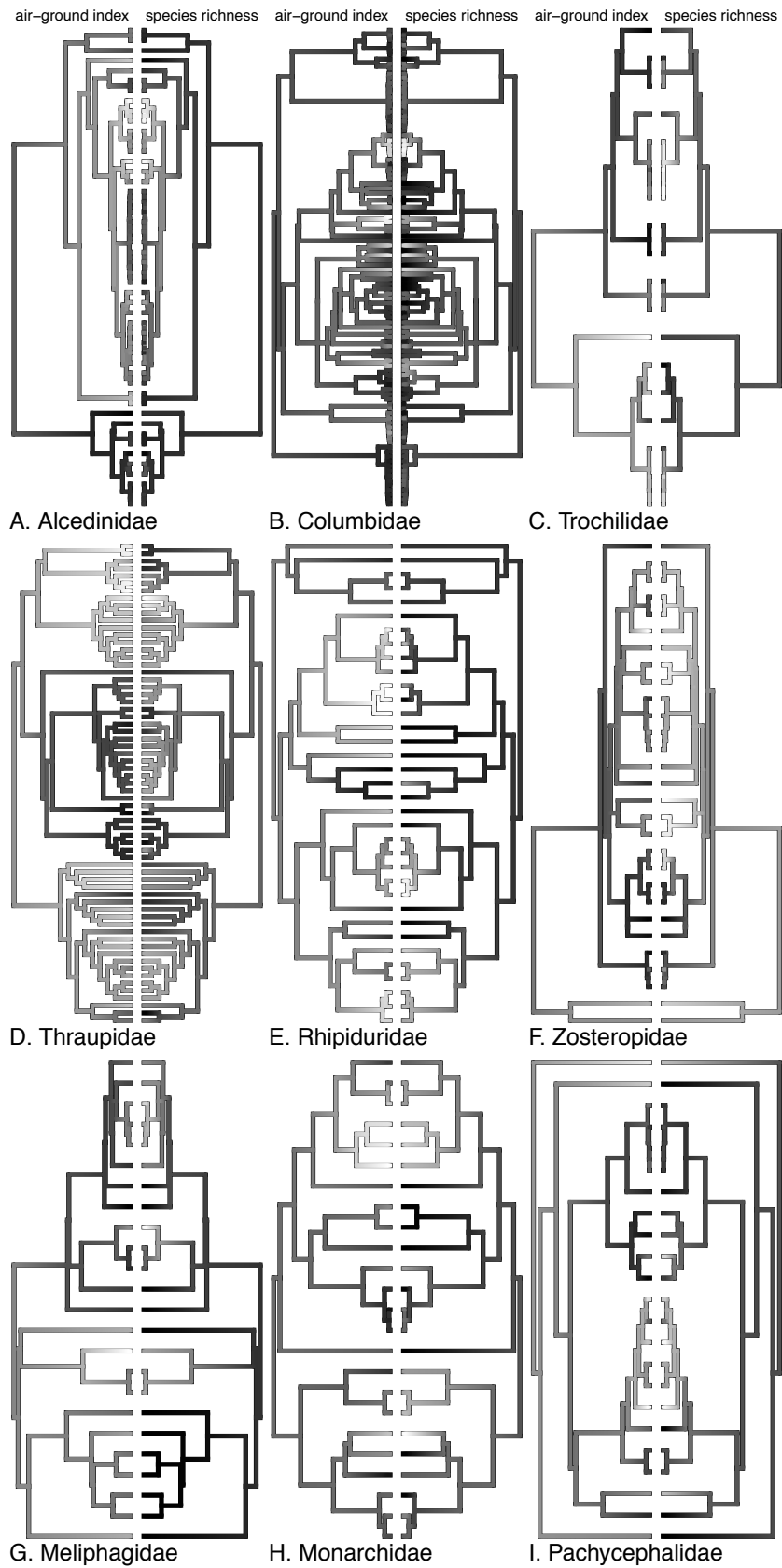
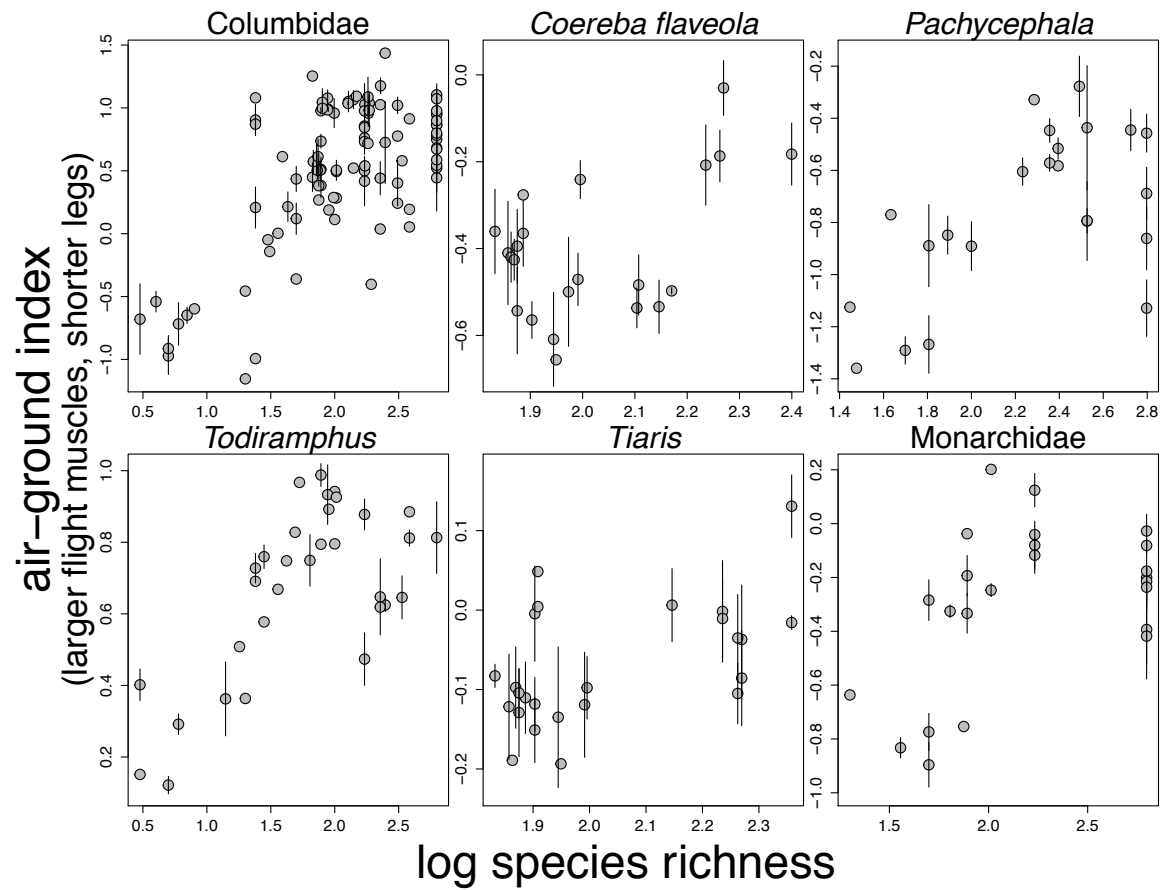


Figure 5: Island species richness is positively correlated with larger flight muscles and shorter legs (Tables 1, S2). The figure shows island population means of the air-ground index and log island landbird species richness for representative taxa. Greater values of the air-ground index indicate larger flight muscles and shorter legs. Each point represents the mean value for one island population. Vertical bars indicate standard deviation from the mean.



Chapter 3: Take-off mechanics in island birds: Functional consequences of evolution toward flightlessness

Abstract

Volant island birds evolve reduced flight muscles and longer legs on islands, but the consequences of this morphology for flight performance are unknown. We tested how reduced flight muscles and longer legs affect take-off performance in birds on the small, depauperate island of Tobago. We found that birds on Tobago had slower maximum velocity and maximum acceleration during take-off relative to conspecifics on the larger island of Trinidad. Initiation of wingbeats occurred later during take-off in populations on the island of Tobago in two species. Across all individuals, birds with smaller flight muscles initiated wingbeats later and achieved peak acceleration earlier during take-off. Lower predation pressures on small, species-poor islands likely permit the slower take-off velocities that result from island birds' reduced flight muscles.

Introduction

The newly proposed 'avian island rule' holds that volant island birds tend to evolve smaller flight muscles and longer legs than their continental relatives, with the degree of reduction greatest on islands of lower species richness (Wright and Steadman 2012; Wright et al. 2015). The ecological causes and functional consequences of this evolutionary pattern are unknown. One hypothesis is that reduced ecological pressures on depauperate islands allow volant birds to reduce their flight muscle size. Pectoral flight muscles are energetically expensive, and the evolution of flightlessness in birds confers substantial energy savings due to the severe atrophy of the pectoralis major (McNab

1994, 2002; McNab and Ellis 2006). It follows that any degree of reduction in flight muscles should provide birds with corresponding energy savings that can be directed toward reproduction, foraging, or investment in other structures. Flight muscle size and leg length evolve in concert because ontogenetic and biomechanical tradeoffs cause wing and leg investment to be negatively correlated (Heers and Dial 2014; Wright et al. 2015). Thus, a reduction in flight muscle size on islands is accompanied by an increase in leg size.

Both flight muscles and legs are important contributors to force production during take-off in birds (Earls 2000; Tobalske et al. 2004; Provini et al. 2012; Heers and Dial 2014). Birds use a leg thrust during take-off to provide acceleration, increasing the initial velocity at which birds need to produce lift. This reduces the aerodynamic power requirements of take-off, because powered flight is particularly energetically expensive at very slow velocities (Tobalske et al. 2003). Longer legs provide a longer lever and should thereby increase the acceleration generated by the leg thrust and decrease the power required of the flight muscles.

The relative effects of body size, leg length, and flight muscle size on take-off mechanics in birds have not been teased apart. Take-off mechanics in general are poorly known in birds and very few studies include more than two species (Bonser and Rayner 1996; Earls 2000; Tobalske and Dial 2000; Provini et al. 2012). It is known that avian taxa differ in their take-off styles. For example, compared to other birds, Rufous Hummingbirds, *Selasphorus rufus*, have slow take-off velocities and less contribution from their legs to take-off velocity. Peak acceleration occurs later and wingbeat initiation earlier in hummingbirds than in the Zebra Finch, *Taeniopygia guttata* (Tobalske et al.

2004), a songbird with longer legs and proportionately smaller flight muscles. It is not certain, however, whether the unique aspects of hummingbird take-offs are due to their short legs, large flight muscles, or small body size.

We tested the functional consequences of island birds' reduced flight muscles and longer legs by comparing wild bird populations on the islands of Trinidad and Tobago. Birds on these islands follow the avian island rule, with birds on smaller, species-poor Tobago having smaller flight muscles and longer legs than conspecifics on Trinidad (Wright and Steadman 2012). None of the seven previously studied species differ in body size between the two islands (Wright and Steadman 2012), allowing us to isolate the effects of shape differences that are due to differential size of the forelimbs and hindlimbs.

Methods

We measured flight kinematics and leg thrust forces for take-offs of wild birds on the islands of Trinidad and Tobago using a custom-built perch and a high-speed video camera. We targeted species occurring regularly on both islands, particularly the hummingbirds *Amazilia tobaci* and *Glaucis hirsuta* (Trochilidae), dove *Leptotila verreauxi* (Columbidae), flycatcher *Mionectes oleagineus* (Tyrannidae), thrush *Turdus nudigenis* (Turdidae), tanager *Thraupis episcopus* (Thraupidae), and Bananaquit *Coereba flaveola* (Thraupidae). We obtained >10 successful flight trials from each of these target species. We also measured take-offs of a wide array of taxa encompassing as much variation in flight morphology as possible, including other hummingbird species

(Trochilidae), jacamars (Galbulidae), antbirds (Thamnophilidae), manakins (Pipridae), flycatchers (Tyrannidae), and tanagers (Thraupidae).

Experimental protocol

We captured wild birds using mist-nets. Birds were kept in cotton bags in the shade for less than 1.5 hours before flight trials, or in wire birdcages with food and water for up to 15 hours. Only frugivores were kept in cages for longer time periods, as they most readily adjusted to eating proffered food, including mangos and bananas.

Hummingbirds were offered sugar water (1 part sugar to 4 parts boiled water) every 15 minutes and were not kept in cages. Other small nectar feeders, such as *Coereba flaveola*, were offered sugar water every 30 minutes. The majority of individuals were in captivity less than an hour before their flight trial.

We built a 2m x 1.5m x 1.5m portable flight cage using mosquito netting and PVC piping. This cage kept wild-caught birds from escaping, but allowed them to safely take-off and fly. Birds flew into the mesh sides without injury. The flight cage contained a custom-built perch 1m above the ground at one end of the flight cage. A high-speed video camera recorded lateral view of the perch from 1m away. An experimenter sat behind the perch and released the bird to sit on the perch. Birds usually took off within 1-2 seconds of release to fly directly away from the experimenter. If they did not, the experimenter clapped or snapped her fingers behind the bird, which almost always resulted in the bird taking off immediately. We chose these conditions because the wild birds responded strongly and rapidly to the perceived threat and attempted to escape. This

method resulted in standardized escape responses from our subjects, important because an individual bird's take-off differs with motivation (Tobalske et al. 2004).

To measure leg thrust, we used a custom-made perch instrumented with strain gauges (Tobalske et al. 2004). On either end of the wooden "perch" rod, two twin-bladed force transducers yielded horizontal and vertical forces, amplified using a strain gauge amplifier. Known masses were used to calibrate the strain-gauge amplifier output from volts into Newtons for the exact location on which the bird was perched. Output from the strain gauge amplifiers were sampled at 1000 Hz and stored for analysis on a laptop computer. High-speed video of take-off from the experimental perch was recorded in lateral view at 500 frames per second. This work was conducted under UNM IACUC protocol number 13-100991-MC.

Biomechanics and kinematics analyses

We defined take-off as the first five wingbeat cycles, beginning during the leg thrust when horizontal force production reaches 5% of the bird's body weight. For each video frame, we digitized the tip of the bill for most species, or the base of the bill for hummingbirds, using MATLAB tools (Hedrick 2008). We used a known scale, a still frame from the video camera recording a ruler on the perch, to convert digitized points into metric coordinates. We plotted position as a function of time, fitted the data with a curve, and differentiated this fitted curve to calculate the bird's velocity and acceleration in R (R Core Team 2012). The accuracy of these analyses were confirmed using a ball-drop acceleration test (Tobalske et al. 2004).

We tested for differences between populations on Trinidad and Tobago in

maximum velocity and acceleration and the timings of wingbeat initiation, peak velocity, and peak acceleration using mixed effects linear models with individual as a random effect and species as a covariate. Statistical analyses were implemented in R (R Core Team 2012) using the package nlme (Pinheiro et al. 2012).

Morphological data

After the experiments, we collected some of the individuals studied and prepared museum skeletal specimens as in (Wright and Steadman 2012; Wright et al. 2014; Wright et al. 2015) to obtain flight muscle data for these individuals. We used mixed effects linear models with individual as a random effect and species as a covariate to test whether body size-corrected flight muscle size predicts maximum velocity and acceleration and the timings of wingbeat initiation, peak velocity, and peak acceleration.

Results

Birds on Trinidad attained greater maximum acceleration during take-off than those on Tobago (linear mixed effects models with individual as a random effect and species as a covariate: $p=0.01$, df: 23; Figure 6). Birds on Trinidad also attained greater maximum velocity during take-off ($p=0.008$, df: 23).

Two of our seven target species, *Amazilia tobaci* and *Mionectes oleagineus*, differed significantly in the timings of the leg thrust and first full wingbeat between the two islands (t-test: *A. tobaci*: $p=0.007$, df: 30; *M. oleagineus*: $p=0.004$, df: 24). In both species, birds began beating their wings earlier in takeoff, relative to when the feet left the perch, on Trinidad than on Tobago (Figure 7). Across all species, relative flight

muscle size correlated with the timing of wingbeat initiation ($p < 0.001$, df: 93; Figure 8), with larger-muscled birds beginning the first wingbeat earlier in take-off. Earlier wingbeats correlated with faster horizontal acceleration ($p = 0.06$, df: 37), but not with vertical acceleration ($p = 0.42$, df: 37).

Flight muscle size correlated with the timing of peak acceleration ($p = 0.008$, df: 21; Figure 9) but not with the timing of peak velocity ($p = 0.87$, df: 21). Birds with larger flight muscles reached peak acceleration later in take-off. We found no evidence for differences between island populations in the timing of maximum acceleration and maximum velocity during take-off ($p > 0.1$, df: 23). There were significant differences among species in the timings of peak acceleration ($p = 0.03$, df: 24), but not in the timings of peak velocity ($p = 0.36$, df: 24).

Flight muscle size correlated negatively with maximum acceleration in a mixed model with both species and body mass as covariates and individual as a random effect ($p < 0.001$, df: 20). Flight muscle size correlated positively with maximum velocity in a similar mixed model ($p = 0.008$, df: 20).

Discussion

Our data demonstrate that a persistent pattern of geographic variation in avian morphology has functional implications for flight performance. Birds on the small, species-poor island of Tobago have evolved smaller flight muscles and longer legs than conspecifics on larger Trinidad (Wright and Steadman 2012). Tobago birds had slower maximum velocity and maximum acceleration during take-off than birds on Trinidad (Figure 6). In two species with smaller flight muscles and longer legs on Tobago (Wright

and Steadman 2012), initiation of wingbeats occurred later during take-off on the island of Tobago (Figure 7). Overall, birds with smaller flight muscles relative to their body size initiated wingbeats later and achieved peak acceleration earlier during take-off.

Birds with smaller flight muscles are more hindlimb-dominant during take-off. Flight muscle investment correlates negatively with hindlimb investment in birds due to ontogenetic and mechanistic tradeoffs (Heers and Dial 2014; Wright et al. 2015). Thus birds with smaller flight muscles are more dependent upon the leg thrust to generate acceleration during take-off. Their legs are longer, providing a longer lever for greater acceleration during the leg thrust. They engage their wings later during take-off, often well after their feet have left the perch (Figure 8). They reach peak acceleration earlier during take-off, often before their feet have left the perch (Figure 9), and in many cases, before their wings have begun to contribute to acceleration at all.

Birds with smaller flight muscles have slower overall take-offs, reaching slower maximum velocities. Conversely, they attain greater maximum accelerations during take-off. This greater acceleration is likely due to a greater contribution from the legs, but further work quantifying relative force generated by the legs vs. the wings is needed. Peak acceleration is typically reached during or shortly after the leg thrust (Figure 9). After peak acceleration, birds continue to accelerate, albeit more slowly. Many individuals begin decelerating within 0.2 seconds of leaving the perch, and therefore reach peak velocity before the end of our take-off period. Thus birds with the fastest maximum acceleration do not necessarily have the fastest maximum take-off velocities.

This work supports the hypothesis that the evolution of small flight muscles and long legs in island birds is caused by reduced predation pressures on islands (Wright and

Steadman 2012; Wright et al. 2015). Slower velocity of take-off would increase susceptibility to predation unless it were accompanied by additional predator-avoidance strategies. Island birds are notorious, however, for their ecological naivety, “island tameness,” and general lack of predator-avoidance behaviors (Darwin 1860; Lack 1983; Quammen 1996). The hummingbird *Amazilia tobaci*, which in this study exhibits differences in take-off mechanics between the islands of Trinidad and Tobago and which has smaller flight muscles on Tobago (Wright and Steadman 2012), exhibits reduced vigilance on Tobago. It tends to perch more in exposed areas and vocalize more often on Tobago than on Trinidad (Feinsinger and Swarm 1982). This study suggests that a biomechanical and behavioral vulnerabilities evolve in parallel. Small-island birds have reduced escape capabilities in part because their smaller flight muscles yield slower take-offs.

Islands of lower species richness tend to have fewer predator species (MacArthur and Wilson 1967; Raffaele et al. 1998; Steadman 2006). When only one or a few raptor species are present on an island, they tend to be generalists (Raffaele et al. 1998; Steadman 2006). Avian specialist predators occur on islands of high species richness and likely exert a higher predation pressure on landbirds for escape abilities than do generalist species. This is the case for the islands of Trinidad and Tobago. Fifteen species of diurnal or crepuscular forest raptors, including species that specialize in predating small birds, such as the Ferruginous Pygmy-owl, *Glaucidium brasilianum*, occur regularly on Trinidad (ffrench 1991). Tobago, however, only hosts two species of diurnal forest raptors, neither of which regularly eats small birds (ffrench 1991). Predators of small- to medium-bodied birds, such as those in this study, generally capture their prey by surprise.

Once the potential prey is airborne, it has a good chance of escape, because small birds generally have better maneuverability than their larger predators. Thus, take-off velocity should play an important role in predator avoidance. We conclude that the paucity of specialist predators on depauperate islands allows birds to reduce their metabolically expensive flight muscles despite the resulting reduction in take-off speed. This mechanism provides a plausible functional explanation for the ‘avian island rule’.

Figure 6: Birds on Trinidad attained greater maximum acceleration (top panel) and greater maximum velocity (bottom panel) during take-off than birds on Tobago. Box width represents relative sample sizes.

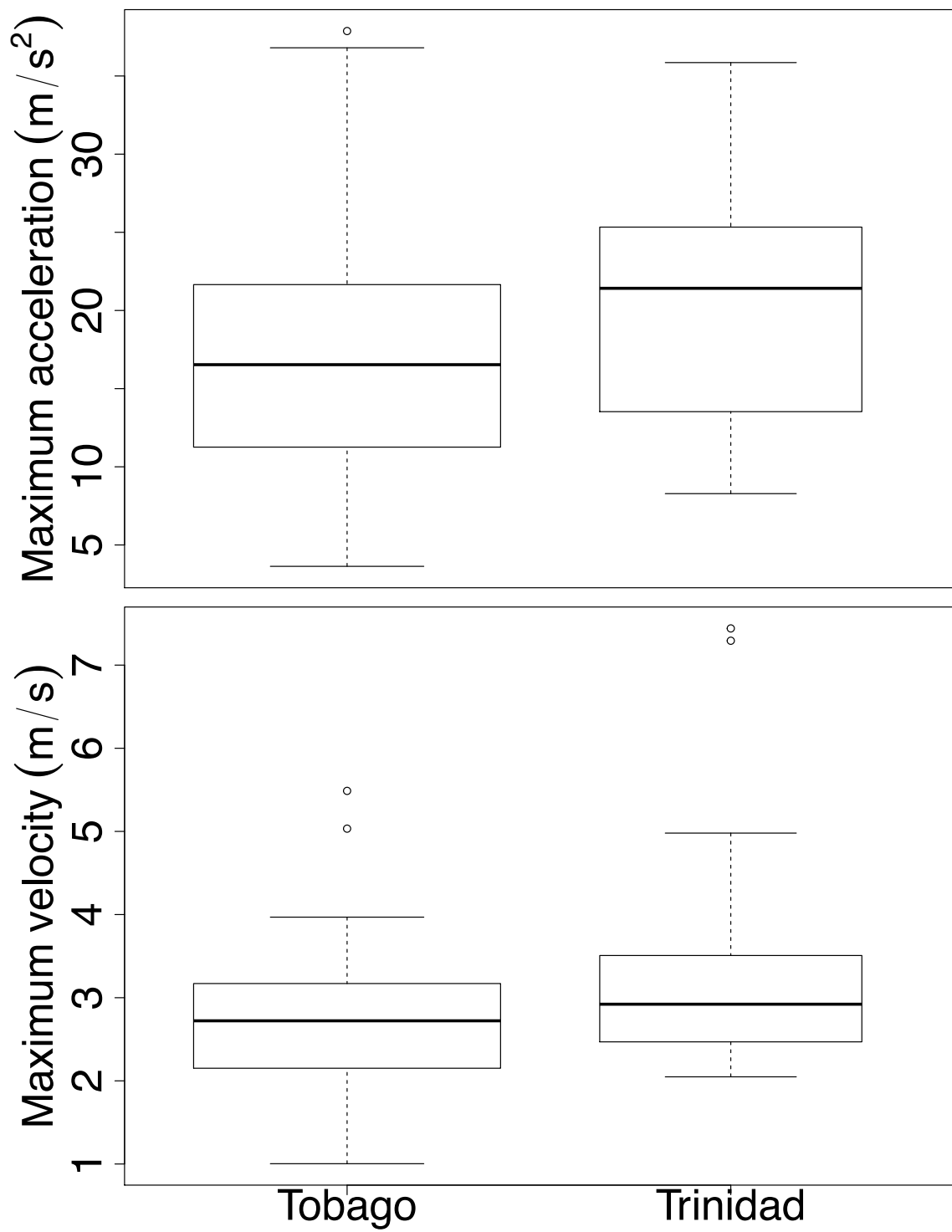


Figure 7: The hummingbird *Amazilia tobaci* and flycatcher *Mionectes oleagineus* begin engaging their wings in take-off later on the island of Tobago than on Trinidad. Y-axis: positive values indicate that the feet leave the perch before the first down wingbeat begins, whereas negative values occur when downward wingbeats begin before the feet leave the perch. Box width represents relative sample sizes.

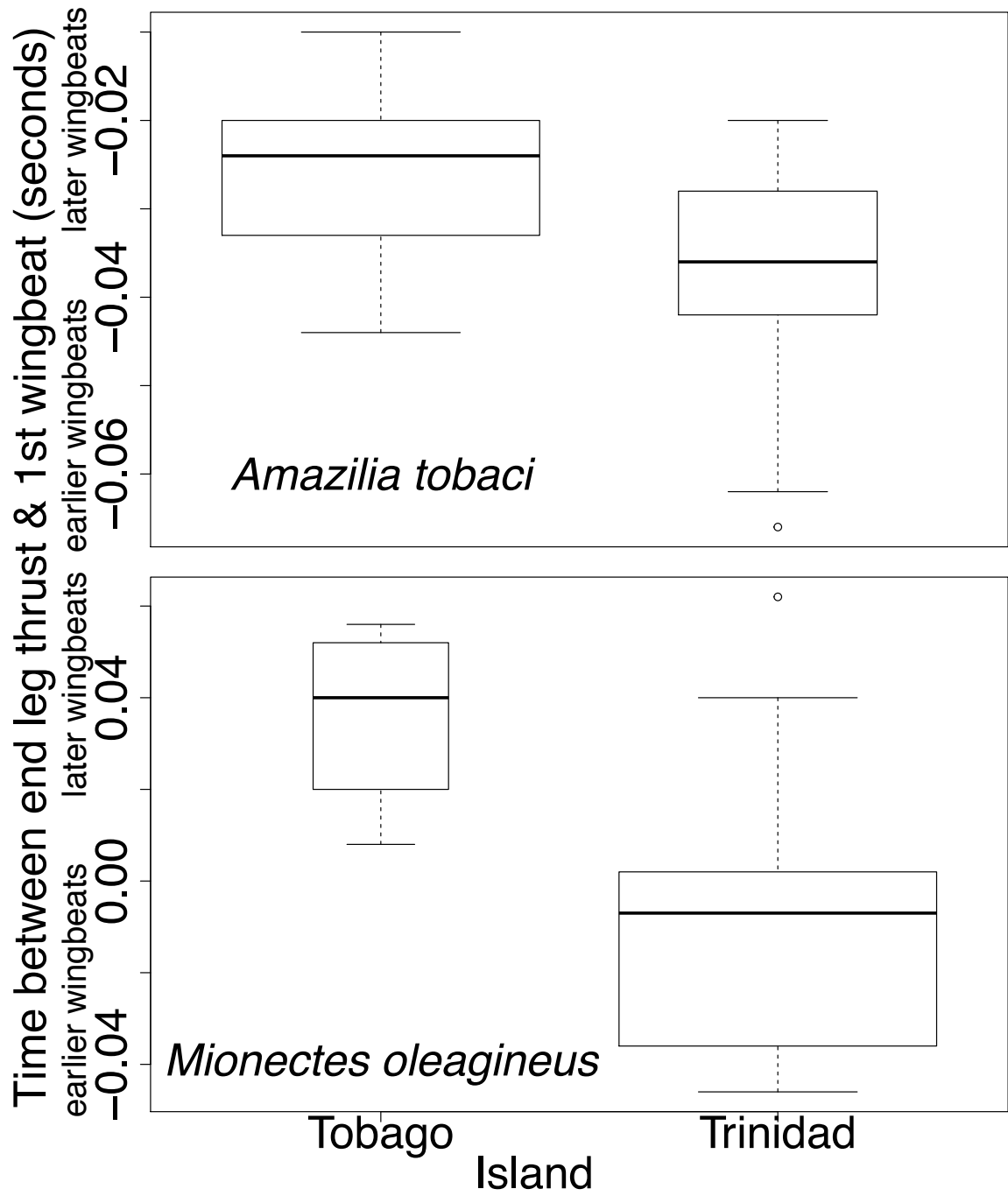


Figure 8: Larger flight muscles correlate with earlier engagement of the wings in take-off. Regression line is from a mixed effects model with individual as a random effect and species as a covariate. X-axis: relative flight muscle size is the percentage of total body mass contributed by the pectoral flight muscles. Y-axis: positive values indicate that the feet left the perch before the first down wingbeat began, whereas negative values occur when downward wingbeats began before the feet left the perch.

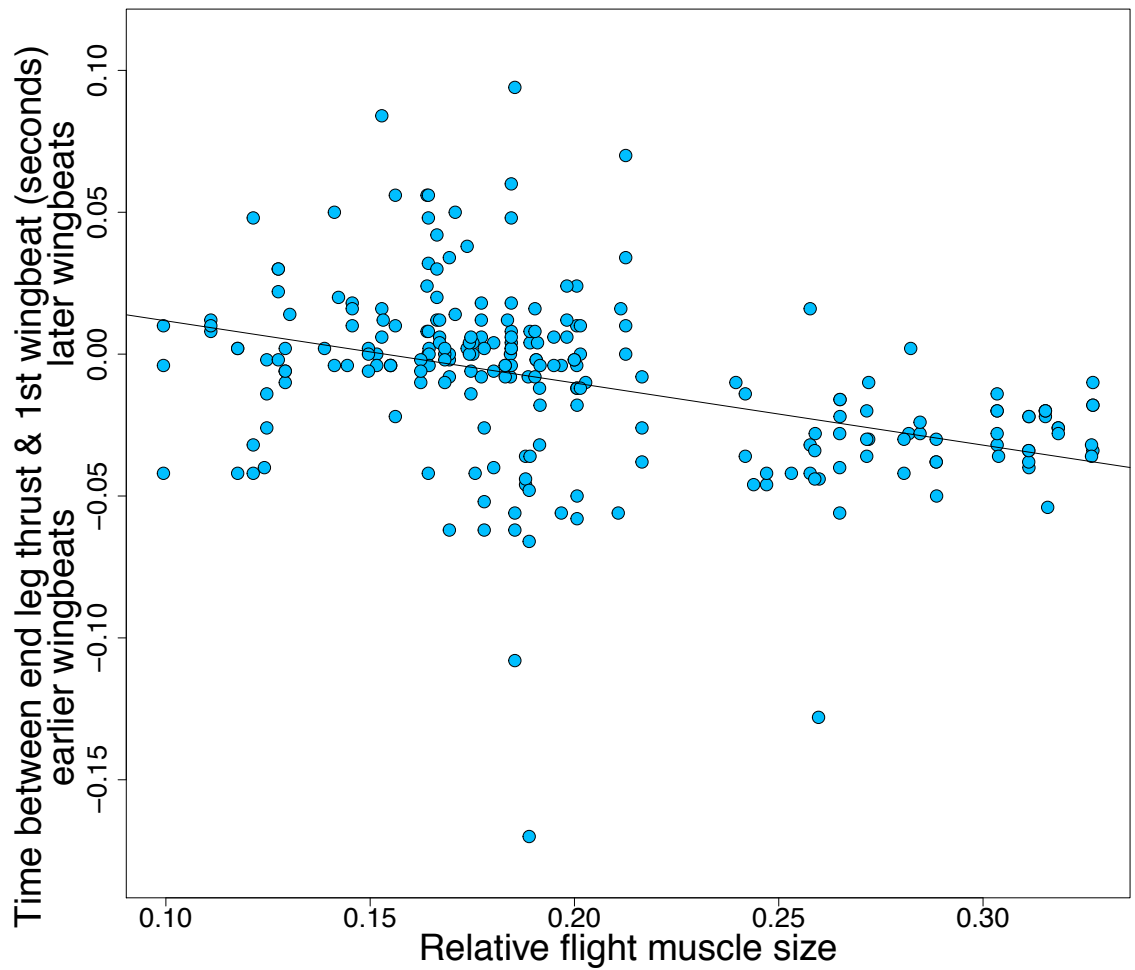
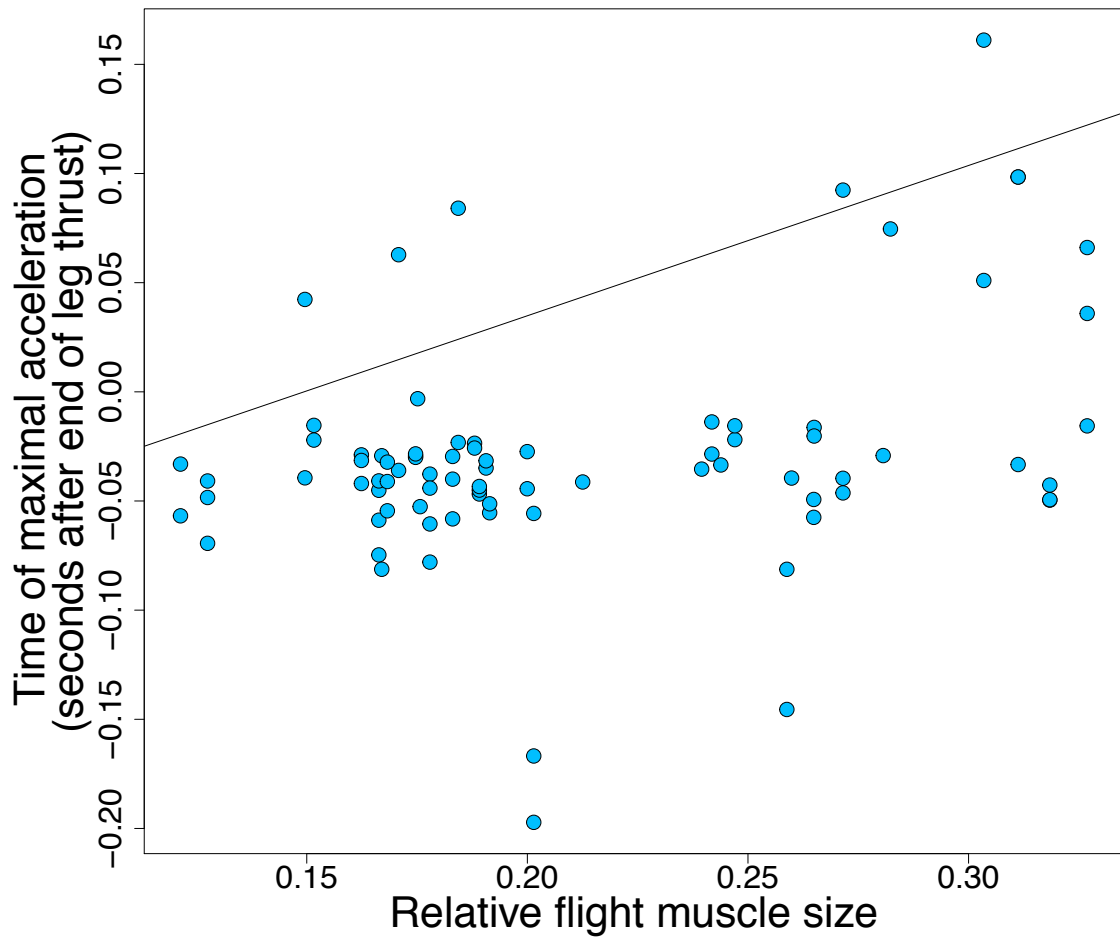


Figure 9: Birds with larger flight muscles achieve peak acceleration later in take-off.

Regression line is from a mixed effects model with individual as a random effect and species as a covariate. X-axis: relative flight muscle size is the percentage of total body mass contributed by the pectoral flight muscles. Y-axis: time is standardized to the time at which the feet left the perch during take-off. Positive values indicate that peak acceleration occurred after the feet left the perch.



Appendix 1: Supplemental Materials for Chapter 1

Table S1: Genome size estimates, museum catalog number, and taxonomic information for each specimen included in this study, sorted alphabetically by order, family, and species. Taxonomy follows (Monge and León-Velarde 1991; Maggiorini et al. 2001) with selected updates (Reeves and Grover 1975; Jürgens et al. 1988).

Order	Family	Species	Catalog number	C-value
Accipitriformes	Accipitridae	<i>Accipiter striatus</i>	MSB:Bird:36209	1.547
Apodiformes	Apodidae	<i>Apus affinis</i>	MSB:Bird:30311	1.380
Apodiformes	Apodidae	<i>Apus caffer</i>	MSB:Bird:30343	1.269
Apodiformes	Apodidae	<i>Apus caffer</i>	MSB:Bird:30344	1.163
Apodiformes	Apodidae	<i>Apus caffer</i>	MSB:Bird:30345	1.175
Apodiformes	Apodidae	<i>Apus caffer</i>	MSB:Bird:30346	1.125
Apodiformes	Apodidae	<i>Chaetura egregia</i>	MSB:Bird:37281	1.167
Apodiformes	Apodidae	<i>Chaetura egregia</i>	MSB:Bird:37282	1.090
Apodiformes	Apodidae	<i>Chaetura vauxi</i>	MSB:Bird:29000	1.209
Apodiformes	Trochilidae	<i>Aglaeactis castelnaudii</i>	MSB:Bird:33102	1.157
Apodiformes	Trochilidae	<i>Aglaeactis castelnaudii</i>	MSB:Bird:34188	1.205
Apodiformes	Trochilidae	<i>Aglaeactis cupripennis</i>	MSB:Bird:35196	1.207
Apodiformes	Trochilidae	<i>Aglaeactis cupripennis</i>	MSB:Bird:35324	1.198
Apodiformes	Trochilidae	<i>Aglaeactis cupripennis</i>	MSB:Bird:36032	1.205
Apodiformes	Trochilidae	<i>Aglaeactis cupripennis</i>	MSB:Bird:36043	1.167
Apodiformes	Trochilidae	<i>Agelaiocercus kingi</i>	MSB:Bird:34568	1.153
Apodiformes	Trochilidae	<i>Amazilia chionogaster</i>	MSB:Bird:33268	1.252
Apodiformes	Trochilidae	<i>Amazilia chionogaster</i>	MSB:Bird:35759	1.279
Apodiformes	Trochilidae	<i>Amazilia chionogaster</i>	MSB:Bird:35760	1.216
Apodiformes	Trochilidae	<i>Amazilia chionogaster</i>	MSB:Bird:35774	1.207
Apodiformes	Trochilidae	<i>Amazilia viridicauda</i>	MSB:Bird:33259	1.268

Apodiformes	Trochilidae	<i>Amazilia viridicauda</i>	MSB:Bird:33261	1.211
Apodiformes	Trochilidae	<i>Amazilia viridicauda</i>	MSB:Bird:33270	1.270
Apodiformes	Trochilidae	<i>Amazilia viridicauda</i>	MSB:Bird:33274	1.262
Apodiformes	Trochilidae	<i>Anthracothorax nigricollis</i>	MSB:Bird:37302	1.100
Apodiformes	Trochilidae	<i>Archilochus alexandri</i>	MSB:Bird:29601	1.184
Apodiformes	Trochilidae	<i>Calypte anna</i>	MSB:Bird:29207	1.139
Apodiformes	Trochilidae	<i>Campylopterus</i>	MSB:Bird:36129	1.179
		<i>villaviscensio</i>		
Apodiformes	Trochilidae	<i>Chalcostigma ruficeps</i>	MSB:Bird:34369	1.182
Apodiformes	Trochilidae	<i>Chalcostigma stanleyi</i>	MSB:Bird:33032	1.202
Apodiformes	Trochilidae	<i>Chalcostigma stanleyi</i>	MSB:Bird:33049	1.224
Apodiformes	Trochilidae	<i>Coeligena torquata</i>	MSB:Bird:31911	1.204
Apodiformes	Trochilidae	<i>Coeligena violifer</i>	MSB:Bird:34661	1.209
Apodiformes	Trochilidae	<i>Colibri thalassinus</i>	MSB:Bird:32514	1.160
Apodiformes	Trochilidae	<i>Colibri thalassinus</i>	MSB:Bird:32702	1.140
Apodiformes	Trochilidae	<i>Doryfera ludovicae</i>	MSB:Bird:36885	1.275
Apodiformes	Trochilidae	<i>Ensifera ensifera</i>	MSB:Bird:33938	1.161
Apodiformes	Trochilidae	<i>Eriocnemis luciani</i>	MSB:Bird:33955	1.221
Apodiformes	Trochilidae	<i>Eriocnemis luciani</i>	MSB:Bird:33997	1.201
Apodiformes	Trochilidae	<i>Eutoxeres condamini</i>	MSB:Bird:36761	1.122
Apodiformes	Trochilidae	<i>Eutoxeres condamini</i>	MSB:Bird:36765	1.117
Apodiformes	Trochilidae	<i>Haplophaedia aureliae</i>	MSB:Bird:36728	1.108
Apodiformes	Trochilidae	<i>Helianthus viola</i>	MSB:Bird:35135	1.128
Apodiformes	Trochilidae	<i>Helianthus viola</i>	MSB:Bird:35175	1.175
Apodiformes	Trochilidae	<i>Helianthus viola</i>	MSB:Bird:35180	1.180
Apodiformes	Trochilidae	<i>Heliodoxa aurescens</i>	MSB:Bird:36498	1.045
Apodiformes	Trochilidae	<i>Heliodoxa aurescens</i>	MSB:Bird:36686	1.129
Apodiformes	Trochilidae	<i>Heliodoxa aurescens</i>	MSB:Bird:36727	1.118
Apodiformes	Trochilidae	<i>Heliodoxa aurescens</i>	MSB:Bird:36855	1.162
Apodiformes	Trochilidae	<i>Heliodoxa rubinoides</i>	MSB:Bird:32494	1.171
Apodiformes	Trochilidae	<i>Heliodoxa rubinoides</i>	MSB:Bird:32542	1.200

Apodiformes	Trochilidae	<i>Helimaster longirostris</i>	MSB:Bird:36912	1.243
Apodiformes	Trochilidae	<i>Helimaster longirostris</i>	MSB:Bird:37073	1.160
Apodiformes	Trochilidae	<i>Hylocharis cyaneus</i>	MSB:Bird:37112	1.175
Apodiformes	Trochilidae	<i>Klais guimeti</i>	MSB:Bird:36149	1.165
Apodiformes	Trochilidae	<i>Klais guimeti</i>	MSB:Bird:36635	1.125
Apodiformes	Trochilidae	<i>Klais guimeti</i>	MSB:Bird:36672	1.123
Apodiformes	Trochilidae	<i>Klais guimeti</i>	MSB:Bird:36861	1.105
Apodiformes	Trochilidae	<i>Lafresnaya lafresnayi</i>	MSB:Bird:35223	1.200
Apodiformes	Trochilidae	<i>Lafresnaya lafresnayi</i>	MSB:Bird:35333	1.283
Apodiformes	Trochilidae	<i>Lesbia nuna</i>	MSB:Bird:35188	1.177
Apodiformes	Trochilidae	<i>Lesbia victoriae</i>	MSB:Bird:36028	1.121
Apodiformes	Trochilidae	<i>Leucippus taczanowskii</i>	MSB:Bird:34065	1.224
Apodiformes	Trochilidae	<i>Leucippus taczanowskii</i>	MSB:Bird:34066	1.237
Apodiformes	Trochilidae	<i>Metallura tyrianthina</i>	MSB:Bird:36046	1.181
Apodiformes	Trochilidae	<i>Myrmia micrura</i>	MSB:Bird:33799	1.286
Apodiformes	Trochilidae	<i>Myrtis fanny</i>	MSB:Bird:34915	1.302
Apodiformes	Trochilidae	<i>Phaethornis guy</i>	MSB:Bird:36598	1.219
Apodiformes	Trochilidae	<i>Phaethornis guy</i>	MSB:Bird:36752	1.212
Apodiformes	Trochilidae	<i>Phaethornis philippii</i>	MSB:Bird:36901	1.176
Apodiformes	Trochilidae	<i>Phaethornis philippii</i>	MSB:Bird:36981	1.210
Apodiformes	Trochilidae	<i>Phaethornis philippii</i>	MSB:Bird:37001	1.127
Apodiformes	Trochilidae	<i>Phaethornis ruber</i>	MSB:Bird:36977	1.131
Apodiformes	Trochilidae	<i>Phaethornis stuarti</i>	MSB:Bird:36687	1.167
Apodiformes	Trochilidae	<i>Phaethornis stuarti</i>	MSB:Bird:36848	1.159
Apodiformes	Trochilidae	<i>Phlogophilus harterti</i>	MSB:Bird:36628	1.196
Apodiformes	Trochilidae	<i>Polyonymus caroli</i>	MSB:Bird:35990	1.148
Apodiformes	Trochilidae	<i>Rhodopsis vesper</i>	MSB:Bird:35436	1.187
Apodiformes	Trochilidae	<i>Rhodopsis vesper</i>	MSB:Bird:35447	1.185
Apodiformes	Trochilidae	<i>Selasphorus platycercus</i>	MSB:Bird:26998	1.092
Apodiformes	Trochilidae	<i>Selasphorus rufus</i>	MSB:Bird:29844	1.151
Apodiformes	Trochilidae	<i>Taphrospilus hypostictus</i>	MSB:Bird:36867	1.136

Apodiformes	Trochilidae	<i>Taphrospilus hypostictus</i>	MSB:Bird:36890	1.176
Apodiformes	Trochilidae	<i>Thaumastura cora</i>	MSB:Bird:32994	1.153
Apodiformes	Trochilidae	<i>Threnetes leucurus</i>	MSB:Bird:36868	1.151
Caprimulgiformes	Caprimulgidae	<i>Caprimulgus nigrescens</i>	MSB:Bird:36288	1.395
Caprimulgiformes	Caprimulgidae	<i>Caprimulgus rufigena</i>	MSB:Bird:30050	1.155
Caprimulgiformes	Caprimulgidae	<i>Chordeiles acutipennis</i>	MSB:Bird:34228	1.453
Caprimulgiformes	Caprimulgidae	<i>Chordeiles acutipennis</i>	MSB:Bird:34229	1.451
Caprimulgiformes	Caprimulgidae	<i>Nyctiphrynus ocellatus</i>	MSB:Bird:36442	1.465
Charadriiformes	Charadriidae	<i>Vanellus coronatus</i>	MSB:Bird:30396	1.677
Charadriiformes	Charadriidae	<i>Vanellus coronatus</i>	MSB:Bird:30397	1.663
Charadriiformes	Turnicidae	<i>Turnix sylvaticus</i>	MSB:Bird:30042	1.258
Ciconiiformes	Scopidae	<i>Scopus umbretta</i>	MSB:Bird:30380	1.398
Ciconiiformes	Scopidae	<i>Scopus umbretta</i>	MSB:Bird:30381	1.311
Ciconiiformes	Threskiornithidae	<i>Bostrychia hagedash</i>	MSB:Bird:30390	1.466
Coliiformes	Coliidae	<i>Colius colius</i>	MSB:Bird:30054	1.467
Coliiformes	Coliidae	<i>Urocolius indicus</i>	MSB:Bird:30056	1.562
Coliiformes	Coliidae	<i>Urocolius indicus</i>	MSB:Bird:30057	1.489
Columbiformes	Columbidae	<i>Geotrygon montana</i>	MSB:Bird:36764	1.506
Columbiformes	Columbidae	<i>Leptotila rufaxilla</i>	MSB:Bird:36832	1.410
Columbiformes	Columbidae	<i>Leptotila verreauxi</i>	MSB:Bird:36605	1.409
Columbiformes	Columbidae	<i>Patagioenas fasciata</i>	MSB:Bird:35195	1.491
Columbiformes	Columbidae	<i>Streptopelia capicola</i>	MSB:Bird:30044	1.409
Columbiformes	Columbidae	<i>Streptopelia senegalensis</i>	MSB:Bird:30045	1.369
Columbiformes	Columbidae	<i>Streptopelia senegalensis</i>	MSB:Bird:30046	1.365
Columbiformes	Columbidae	<i>Zenaida auriculata</i>	MSB:Bird:34976	1.408
Coraciiformes	Alcedinidae	<i>Halcyon albiventris</i>	MSB:Bird:30063	1.580
Coraciiformes	Coraciidae	<i>Coracias garrulus</i>	MSB:Bird:30064	1.280
Coraciiformes	Meropidae	<i>Merops apiaster</i>	MSB:Bird:30069	1.320
Coraciiformes	Meropidae	<i>Merops bullockoides</i>	MSB:Bird:30067	1.335
Coraciiformes	Meropidae	<i>Merops bullockoides</i>	MSB:Bird:30068	1.406
Coraciiformes	Momotidae	<i>Baryphthengus martii</i>	MSB:Bird:27757	1.500

Coraciiformes	Momotidae	<i>Momotus momota</i>	MSB:Bird:37262	1.520
Coraciiformes	Phoeniculidae	<i>Phoeniculus purpureus</i>	MSB:Bird:30051	1.319
Coraciiformes	Phoeniculidae	<i>Rhinopomastus cyanomelas</i>	MSB:Bird:30347	1.131
Coraciiformes	Phoeniculidae	<i>Rhinopomastus cyanomelas</i>	MSB:Bird:30348	1.125
Coraciiformes	Upupidae	<i>Upupa epops</i>	MSB:Bird:30312	1.276
Cuculiformes	Cuculidae	<i>Chrysococcyx caprius</i>	MSB:Bird:30316	1.442
Cuculiformes	Cuculidae	<i>Chrysococcyx caprius</i>	MSB:Bird:30317	1.446
Cuculiformes	Cuculidae	<i>Clamator jacobinus</i>	MSB:Bird:30321	1.399
Cuculiformes	Cuculidae	<i>Crotophaga ani</i>	MSB:Bird:36690	1.381
Cuculiformes	Cuculidae	<i>Crotophaga ani</i>	MSB:Bird:37244	1.291
Cuculiformes	Cuculidae	<i>Crotophaga sulcirostris</i>	MSB:Bird:33879	1.328
Cuculiformes	Cuculidae	<i>Neomorphus geoffroyi</i>	MSB:Bird:36662	1.507
Falconiformes	Falconidae	<i>Falco sparverius</i>	MSB:Bird:35898	1.430
Falconiformes	Falconidae	<i>Falco sparverius</i>	MSB:Bird:35929	1.434
Falconiformes	Falconidae	<i>Micrastur ruficollis</i>	MSB:Bird:36769	1.573
Galliformes	Phasianidae	<i>Francolinus natalensis</i>	MSB:Bird:30384	1.215
Galliformes	Phasianidae	<i>Francolinus swainsonii</i>	MSB:Bird:30385	1.205
Galliformes	Phasianidae	<i>Francolinus swainsonii</i>	MSB:Bird:30386	1.212
Galliformes	Phasianidae	<i>Numida meleagris</i>	MSB:Bird:30382	1.232
Galliformes	Phasianidae	<i>Numida meleagris</i>	MSB:Bird:30383	1.249
Passeriformes	Acrocephalidae	<i>Acrocephalus baeticatus</i>	MSB:Bird:30202	1.333
Passeriformes	Acrocephalidae	<i>Acrocephalus baeticatus</i>	MSB:Bird:30203	1.329
Passeriformes	Acrocephalidae	<i>Hippolais icterina</i>	MSB:Bird:30199	1.293
Passeriformes	Acrocephalidae	<i>Hippolais icterina</i>	MSB:Bird:30200	1.282
Passeriformes	Alaudidae	<i>Calendulauda sabota</i>	MSB:Bird:30367	1.279
Passeriformes	Alaudidae	<i>Calendulauda sabota</i>	MSB:Bird:30368	1.213
Passeriformes	Cardinalidae	<i>Cyanocompsa cyanoides</i>	MSB:Bird:37162	1.342
Passeriformes	Cardinalidae	<i>Pheucticus aureoventris</i>	MSB:Bird:35704	1.511
Passeriformes	Cardinalidae	<i>Pheucticus aureoventris</i>	MSB:Bird:35705	1.405
Passeriformes	Cardinalidae	<i>Pheucticus chrysogaster</i>	MSB:Bird:35389	1.454
Passeriformes	Cinclidae	<i>Cinclus leucocephalus</i>	MSB:Bird:35883	1.275

Passeriformes	Cisticolidae	<i>Cisticola aridulus</i>	MSB:Bird:30171	1.240
Passeriformes	Cisticolidae	<i>Cisticola chiniana</i>	MSB:Bird:30177	1.239
Passeriformes	Cisticolidae	<i>Cisticola chiniana</i>	MSB:Bird:30178	1.217
Passeriformes	Cisticolidae	<i>Cisticola fulvicapilla</i>	MSB:Bird:30172	1.152
Passeriformes	Cisticolidae	<i>Cisticola juncidis</i>	MSB:Bird:30181	1.201
Passeriformes	Cisticolidae	<i>Cisticola juncidis</i>	MSB:Bird:30182	1.127
Passeriformes	Cisticolidae	<i>Cisticola subruficapilla</i>	MSB:Bird:30169	1.149
Passeriformes	Cisticolidae	<i>Cisticola subruficapilla</i>	MSB:Bird:30170	1.094
Passeriformes	Cisticolidae	<i>Cisticola textrix</i>	MSB:Bird:30183	1.147
Passeriformes	Cisticolidae	<i>Cisticola textrix</i>	MSB:Bird:30184	1.173
Passeriformes	Cisticolidae	<i>Prinia flavicans</i>	MSB:Bird:30160	1.276
Passeriformes	Cisticolidae	<i>Prinia flavicans</i>	MSB:Bird:30161	1.270
Passeriformes	Cisticolidae	<i>Prinia maculosa</i>	MSB:Bird:30163	0.953
Passeriformes	Cisticolidae	<i>Prinia maculosa</i>	MSB:Bird:30164	1.133
Passeriformes	Conopophagidae	<i>Conopophaga castaneiceps</i>	MSB:Bird:36167	1.449
Passeriformes	Cotingidae	<i>Ampelioides tschudii</i>	MSB:Bird:36865	1.624
Passeriformes	Cotingidae	<i>Ampelion rubrocristatus</i>	MSB:Bird:35262	1.353
Passeriformes	Cotingidae	<i>Ampelion rubrocristatus</i>	MSB:Bird:35998	1.330
Passeriformes	Cotingidae	<i>Lipaugus vociferans</i>	MSB:Bird:37260	1.300
Passeriformes	Cotingidae	<i>Pipreola frontalis</i>	MSB:Bird:36210	1.236
Passeriformes	Cotingidae	<i>Pipreola frontalis</i>	MSB:Bird:36545	1.499
Passeriformes	Cotingidae	<i>Querula purpurata</i>	MSB:Bird:37312	1.671
Passeriformes	Cotingidae	<i>Querula purpurata</i>	MSB:Bird:37313	1.580
Passeriformes	Cotingidae	<i>Snowornis cryptolophus</i>	MSB:Bird:36193	1.420
Passeriformes	Cotingidae	<i>Snowornis subalaris</i>	MSB:Bird:36152	1.295
Passeriformes	Cotingidae	<i>Snowornis subalaris</i>	MSB:Bird:36334	1.247
Passeriformes	Dicruridae	<i>Dicrurus adsimilis</i>	MSB:Bird:30081	1.129
Passeriformes	Emberizidae	<i>Emberiza flaviventris</i>	MSB:Bird:30127	1.379
Passeriformes	Emberizidae	<i>Emberiza tahapisi</i>	MSB:Bird:30375	1.268
Passeriformes	Emberizidae	<i>Emberiza tahapisi</i>	MSB:Bird:30376	1.237
Passeriformes	Estrildidae	<i>Estrilda astrild</i>	MSB:Bird:30393	1.198

Passeriformes	Estrildidae	<i>Estrilda astrild</i>	MSB:Bird:30394	1.195
Passeriformes	Estrildidae	<i>Lagonosticta rhodopareia</i>	MSB:Bird:30264	1.623
Passeriformes	Estrildidae	<i>Lagonosticta senegala</i>	MSB:Bird:30391	1.306
Passeriformes	Estrildidae	<i>Lagonosticta senegala</i>	MSB:Bird:30392	1.215
Passeriformes	Estrildidae	<i>Ortygospiza atricollis</i>	MSB:Bird:30398	1.371
Passeriformes	Estrildidae	<i>Pytilia melba</i>	MSB:Bird:30296	1.422
Passeriformes	Estrildidae	<i>Quelea quelea</i>	MSB:Bird:30253	1.251
Passeriformes	Estrildidae	<i>Uraeginthus angolensis</i>	MSB:Bird:30260	1.292
Passeriformes	Estrildidae	<i>Uraeginthus angolensis</i>	MSB:Bird:30261	1.252
Passeriformes	Estrildidae	<i>Uraeginthus granatinus</i>	MSB:Bird:30258	1.377
Passeriformes	Estrildidae	<i>Uraeginthus granatinus</i>	MSB:Bird:30259	1.182
Passeriformes	Formicariidae	<i>Chamaeza campanisona</i>	MSB:Bird:36283	1.276
Passeriformes	Formicariidae	<i>Chamaeza campanisona</i>	MSB:Bird:36355	1.287
Passeriformes	Fringillidae	<i>Euphonia lanirostris</i>	MSB:Bird:34311	1.240
Passeriformes	Fringillidae	<i>Euphonia lanirostris</i>	MSB:Bird:34329	1.268
Passeriformes	Fringillidae	<i>Leucosticte tephrocotis</i>	MSB:Bird:30440	1.313
Passeriformes	Fringillidae	<i>Serinus atrogularis</i>	MSB:Bird:30299	1.505
Passeriformes	Fringillidae	<i>Serinus atrogularis</i>	MSB:Bird:30300	1.500
Passeriformes	Fringillidae	<i>Serinus flaviventris</i>	MSB:Bird:30303	1.213
Passeriformes	Fringillidae	<i>Serinus flaviventris</i>	MSB:Bird:30304	1.250
Passeriformes	Fringillidae	<i>Sporagra uropygialis</i>	MSB:Bird:36003	1.394
Passeriformes	Furnariidae	<i>Ancistrops strigilatus</i>	MSB:Bird:36432	1.431
Passeriformes	Furnariidae	<i>Asthenes dorbignyi</i>	MSB:Bird:35101	1.266
Passeriformes	Furnariidae	<i>Asthenes dorbignyi</i>	MSB:Bird:35706	1.325
Passeriformes	Furnariidae	<i>Asthenes humilis</i>	MSB:Bird:34199	1.316
Passeriformes	Furnariidae	<i>Asthenes humilis</i>	MSB:Bird:34200	1.298
Passeriformes	Furnariidae	<i>Asthenes ottonis</i>	MSB:Bird:35845	1.311
Passeriformes	Furnariidae	<i>Asthenes virgata</i>	MSB:Bird:34166	1.441
Passeriformes	Furnariidae	<i>Automolus rubiginosus</i>	MSB:Bird:36285	1.301
Passeriformes	Furnariidae	<i>Automolus rubiginosus</i>	MSB:Bird:36457	1.425
Passeriformes	Furnariidae	<i>Campylorhamphus</i>	MSB:Bird:36197	1.226

<i>trochilirostris</i>				
Passeriformes	Furnariidae	<i>Campylorhamphus</i>	MSB:Bird:36325	1.169
<i>trochilirostris</i>				
Passeriformes	Furnariidae	<i>Cinclodes albidiventris</i>	MSB:Bird:28170	1.367
Passeriformes	Furnariidae	<i>Cranioleuca albicapilla</i>	MSB:Bird:33915	1.218
Passeriformes	Furnariidae	<i>Cranioleuca albicapilla</i>	MSB:Bird:35871	1.293
Passeriformes	Furnariidae	<i>Cranioleuca antisensis</i>	MSB:Bird:35307	1.336
Passeriformes	Furnariidae	<i>Cranioleuca marcapatae</i>	MSB:Bird:34431	1.271
Passeriformes	Furnariidae	<i>Cranioleuca marcapatae</i>	MSB:Bird:34446	1.282
Passeriformes	Furnariidae	<i>Deconychura longicauda</i>	MSB:Bird:36709	1.262
Passeriformes	Furnariidae	<i>Dendrocincla fuliginosa</i>	MSB:Bird:36447	1.311
Passeriformes	Furnariidae	<i>Dendrocincla merula</i>	MSB:Bird:37130	1.160
Passeriformes	Furnariidae	<i>Dendrocolaptes picumnus</i>	MSB:Bird:36834	1.152
Passeriformes	Furnariidae	<i>Geositta maritima</i>	MSB:Bird:35450	1.292
Passeriformes	Furnariidae	<i>Geositta maritima</i>	MSB:Bird:35452	1.279
Passeriformes	Furnariidae	<i>Glyphorhynchus spirurus</i>	MSB:Bird:37179	1.141
Passeriformes	Furnariidae	<i>Lepidocolaptes souleyetii</i>	MSB:Bird:33830	1.255
Passeriformes	Furnariidae	<i>Lepidocolaptes souleyetii</i>	MSB:Bird:33831	1.257
Passeriformes	Furnariidae	<i>Leptasthenura striata</i>	MSB:Bird:35097	1.239
Passeriformes	Furnariidae	<i>Leptasthenura striata</i>	MSB:Bird:35099	1.290
Passeriformes	Furnariidae	<i>Leptasthenura xenothorax</i>	MSB:Bird:34028	1.319
Passeriformes	Furnariidae	<i>Leptasthenura xenothorax</i>	MSB:Bird:34031	1.276
Passeriformes	Furnariidae	<i>Philydor erythrocercum</i>	MSB:Bird:36782	1.247
Passeriformes	Furnariidae	<i>Philydor erythrocercum</i>	MSB:Bird:37213	1.163
Passeriformes	Furnariidae	<i>Sclerurus caudacutus</i>	MSB:Bird:36440	1.347
Passeriformes	Furnariidae	<i>Sclerurus mexicanus</i>	MSB:Bird:36338	1.273
Passeriformes	Furnariidae	<i>Synallaxis gujanensis</i>	MSB:Bird:36630	1.347
Passeriformes	Furnariidae	<i>Synallaxis gujanensis</i>	MSB:Bird:36702	1.352
Passeriformes	Furnariidae	<i>Synallaxis rutilans</i>	MSB:Bird:37225	1.418
Passeriformes	Furnariidae	<i>Synallaxis stictothorax</i>	MSB:Bird:33820	1.279
Passeriformes	Furnariidae	<i>Synallaxis stictothorax</i>	MSB:Bird:33833	1.334

Passeriformes	Furnariidae	<i>Syndactyla rufosuperciliata</i>	MSB:Bird:31918	1.289
Passeriformes	Furnariidae	<i>Syndactyla subularis</i>	MSB:Bird:36173	1.125
Passeriformes	Furnariidae	<i>Syndactyla subularis</i>	MSB:Bird:36220	1.221
Passeriformes	Furnariidae	<i>Upucerthia albigula</i>	MSB:Bird:35488	1.277
Passeriformes	Furnariidae	<i>Xiphorhynchus ocellatus</i>	MSB:Bird:36700	1.381
Passeriformes	Grallariidae	<i>Grallaria andicolus</i>	MSB:Bird:36030	1.284
Passeriformes	Grallariidae	<i>Grallaria ruficapilla</i>	MSB:Bird:35251	1.386
Passeriformes	Grallariidae	<i>Grallaria squamigera</i>	MSB:Bird:33988	1.429
Passeriformes	Hirundinidae	<i>Cecropis cucullata</i>	MSB:Bird:30084	1.423
Passeriformes	Hirundinidae	<i>Cecropis semirufa</i>	MSB:Bird:30085	1.414
Passeriformes	Hirundinidae	<i>Cecropis semirufa</i>	MSB:Bird:30086	1.309
Passeriformes	Hirundinidae	<i>Hirundo dimidiata</i>	MSB:Bird:30370	1.390
Passeriformes	Hirundinidae	<i>Hirundo dimidiata</i>	MSB:Bird:30371	1.429
Passeriformes	Hirundinidae	<i>Pygochelidon cyanoleuca</i>	MSB:Bird:35280	1.433
Passeriformes	Hirundinidae	<i>Pygochelidon cyanoleuca</i>	MSB:Bird:35315	1.467
Passeriformes	Hirundinidae	<i>Stelgidopteryx serripennis</i>	MSB:Bird:29784	1.361
Passeriformes	Icteridae	<i>Icterus graceannae</i>	MSB:Bird:33881	1.308
Passeriformes	Icteridae	<i>Icterus graceannae</i>	MSB:Bird:33883	1.301
Passeriformes	Icteridae	<i>Molothrus bonariensis</i>	MSB:Bird:35059	1.507
Passeriformes	Icteridae	<i>Psarocolius angustifrons</i>	MSB:Bird:36699	1.349
Passeriformes	Icteridae	<i>Sturnella bellicosa</i>	MSB:Bird:35042	1.448
Passeriformes	Laniidae	<i>Lanius collurio</i>	MSB:Bird:30091	1.172
Passeriformes	Laniidae	<i>Lanius collurio</i>	MSB:Bird:30092	1.252
Passeriformes	Laniidae	<i>Lanius minor</i>	MSB:Bird:30095	1.274
Passeriformes	Laniidae	<i>Urolestes melanoleucus</i>	MSB:Bird:30372	1.199
Passeriformes	Laniidae	<i>Urolestes melanoleucus</i>	MSB:Bird:30373	1.174
Passeriformes	Macrosphenidae	<i>Sylvietta rufescens</i>	MSB:Bird:30154	1.331
Passeriformes	Macrosphenidae	<i>Sylvietta rufescens</i>	MSB:Bird:30155	1.298
Passeriformes	Malaconotidae	<i>Laniarius atrococcineus</i>	MSB:Bird:30093	1.288
Passeriformes	Malaconotidae	<i>Laniarius atrococcineus</i>	MSB:Bird:30094	1.297
Passeriformes	Malaconotidae	<i>Nilaus afer</i>	MSB:Bird:30096	1.089

Passeriformes	Malaconotidae	<i>Nilaus afer</i>	MSB:Bird:30097	1.271
Passeriformes	Malaconotidae	<i>Tchagra australis</i>	MSB:Bird:30362	1.172
Passeriformes	Malaconotidae	<i>Tchagra australis</i>	MSB:Bird:30363	1.218
Passeriformes	Mimidae	<i>Mimus longicaudatus</i>	MSB:Bird:33695	1.292
Passeriformes	Mimidae	<i>Mimus longicaudatus</i>	MSB:Bird:34666	1.347
Passeriformes	Motacillidae	<i>Anthus cinnamomeus</i>	MSB:Bird:30206	1.285
Passeriformes	Motacillidae	<i>Anthus crenatus</i>	MSB:Bird:30210	1.163
Passeriformes	Motacillidae	<i>Anthus crenatus</i>	MSB:Bird:30211	1.205
Passeriformes	Motacillidae	<i>Anthus similis</i>	MSB:Bird:30207	1.250
Passeriformes	Motacillidae	<i>Anthus similis</i>	MSB:Bird:30208	1.273
Passeriformes	Motacillidae	<i>Macronyx capensis</i>	MSB:Bird:30114	1.266
Passeriformes	Motacillidae	<i>Macronyx capensis</i>	MSB:Bird:30115	1.363
Passeriformes	Motacillidae	<i>Motacilla capensis</i>	MSB:Bird:30117	0.926
Passeriformes	Motacillidae	<i>Motacilla capensis</i>	MSB:Bird:30118	1.183
Passeriformes	Muscicapidae	<i>Bradornis mariquensis</i>	MSB:Bird:30123	1.313
Passeriformes	Muscicapidae	<i>Cercomela familiaris</i>	MSB:Bird:30204	1.228
Passeriformes	Muscicapidae	<i>Cercomela familiaris</i>	MSB:Bird:30205	1.218
Passeriformes	Muscicapidae	<i>Cercotrichas coryphaeus</i>	MSB:Bird:30119	1.331
Passeriformes	Muscicapidae	<i>Cercotrichas coryphaeus</i>	MSB:Bird:30120	1.356
Passeriformes	Muscicapidae	<i>Cercotrichas paena</i>	MSB:Bird:30193	1.270
Passeriformes	Muscicapidae	<i>Cercotrichas paena</i>	MSB:Bird:30194	1.187
Passeriformes	Muscicapidae	<i>Monticola brevipes</i>	MSB:Bird:30135	1.388
Passeriformes	Muscicapidae	<i>Muscicapa striata</i>	MSB:Bird:30152	1.475
Passeriformes	Muscicapidae	<i>Muscicapa striata</i>	MSB:Bird:30153	1.441
Passeriformes	Muscicapidae	<i>Myrmecocichla formicivora</i>	MSB:Bird:30133	1.181
Passeriformes	Muscicapidae	<i>Myrmecocichla formicivora</i>	MSB:Bird:30134	1.221
Passeriformes	Muscicapidae	<i>Oenanthe monticola</i>	MSB:Bird:30136	1.239
Passeriformes	Muscicapidae	<i>Sigelus silens</i>	MSB:Bird:30128	1.354
Passeriformes	Muscicapidae	<i>Sigelus silens</i>	MSB:Bird:30129	1.407

Passeriformes	Paridae	<i>Baeolophus inornatus</i>	MSB:Bird:29202	1.342
Passeriformes	Paridae	<i>Baeolophus inornatus</i>	MSB:Bird:29204	1.292
Passeriformes	Paridae	<i>Parus cinerascens</i>	MSB:Bird:30185	1.207
Passeriformes	Paridae	<i>Parus cinerascens</i>	MSB:Bird:30186	1.213
Passeriformes	Parulidae	<i>Basileuterus bivittatus</i>	MSB:Bird:36644	1.447
Passeriformes	Parulidae	<i>Basileuterus bivittatus</i>	MSB:Bird:36666	1.475
Passeriformes	Parulidae	<i>Basileuterus trifasciatus</i>	MSB:Bird:35142	1.419
Passeriformes	Parulidae	<i>Basileuterus trifasciatus</i>	MSB:Bird:35372	1.402
Passeriformes	Parulidae	<i>Basileuterus tristriatus</i>	MSB:Bird:36146	1.452
Passeriformes	Parulidae	<i>Cardellina canadensis</i>	MSB:Bird:35755	1.490
Passeriformes	Parulidae	<i>Myioborus melanocephalus</i>	MSB:Bird:32101	1.396
Passeriformes	Parulidae	<i>Myioborus melanocephalus</i>	MSB:Bird:34428	1.368
Passeriformes	Parulidae	<i>Myioborus miniatus</i>	MSB:Bird:35235	1.372
Passeriformes	Parulidae	<i>Myioborus miniatus</i>	MSB:Bird:35407	1.408
Passeriformes	Parulidae	<i>Setophaga pitayumi</i>	MSB:Bird:34300	1.457
Passeriformes	Parulidae	<i>Setophaga pitayumi</i>	MSB:Bird:36286	1.411
Passeriformes	Passerellidae	<i>Ammodramus aurifrons</i>	MSB:Bird:36603	1.344
Passeriformes	Passerellidae	<i>Ammodramus aurifrons</i>	MSB:Bird:36604	1.361
Passeriformes	Passerellidae	<i>Arremon assimilis</i>	MSB:Bird:35176	1.663
Passeriformes	Passerellidae	<i>Arremon assimilis</i>	MSB:Bird:35215	1.633
Passeriformes	Passerellidae	<i>Arremon brunneinucha</i>	MSB:Bird:36147	1.367
Passeriformes	Passerellidae	<i>Arremon brunneinucha</i>	MSB:Bird:36230	1.372
Passeriformes	Passerellidae	<i>Arremon taciturnus</i>	MSB:Bird:36653	1.567
Passeriformes	Passerellidae	<i>Arremon taciturnus</i>	MSB:Bird:36747	1.517
Passeriformes	Passerellidae	<i>Atlapetes canigenis</i>	MSB:Bird:34430	1.556
Passeriformes	Passerellidae	<i>Atlapetes forbesi</i>	MSB:Bird:33992	1.331
Passeriformes	Passerellidae	<i>Atlapetes forbesi</i>	MSB:Bird:33993	1.356
Passeriformes	Passerellidae	<i>Atlapetes rufigenis</i>	MSB:Bird:34961	1.403
Passeriformes	Passerellidae	<i>Atlapetes rufigenis</i>	MSB:Bird:34962	1.301
Passeriformes	Passerellidae	<i>Atlapetes seebohmi</i>	MSB:Bird:35335	1.516
Passeriformes	Passerellidae	<i>Atlapetes seebohmi</i>	MSB:Bird:36012	1.392

Passeriformes	Passerellidae	<i>Chlorospingus flavigularis</i>	MSB:Bird:36360	1.446
Passeriformes	Passerellidae	<i>Passerculus sandwichensis</i>	MSB:Bird:40259	1.153
Passeriformes	Passerellidae	<i>Rhynchospiza stolzmanni</i>	MSB:Bird:33703	1.444
Passeriformes	Passerellidae	<i>Rhynchospiza stolzmanni</i>	MSB:Bird:33746	1.421
Passeriformes	Passeridae	<i>Passer diffusus</i>	MSB:Bird:30108	1.329
Passeriformes	Passeridae	<i>Passer diffusus</i>	MSB:Bird:30109	1.292
Passeriformes	Passeridae	<i>Passer melanurus</i>	MSB:Bird:30106	1.316
Passeriformes	Passeridae	<i>Passer melanurus</i>	MSB:Bird:30107	1.307
Passeriformes	Pipridae	<i>Chiroxiphia boliviana</i>	MSB:Bird:36771	1.230
Passeriformes	Pipridae	<i>Chiroxiphia pareola</i>	MSB:Bird:37275	1.236
Passeriformes	Pipridae	<i>Lepidothrix</i> <i>coeruleocapilla</i>	MSB:Bird:36767	1.202
Passeriformes	Pipridae	<i>Lepidothrix</i> <i>coeruleocapilla</i>	MSB:Bird:36815	1.249
Passeriformes	Pipridae	<i>Lepidothrix</i> <i>coeruleocapilla</i>	MSB:Bird:36831	1.291
Passeriformes	Pipridae	<i>Lepidothrix coronata</i>	MSB:Bird:36961	1.228
Passeriformes	Pipridae	<i>Lepidothrix coronata</i>	MSB:Bird:37232	1.142
Passeriformes	Pipridae	<i>Lepidothrix isidorei</i>	MSB:Bird:36125	1.221
Passeriformes	Pipridae	<i>Lepidothrix isidorei</i>	MSB:Bird:36133	1.273
Passeriformes	Pipridae	<i>Lepidothrix isidorei</i>	MSB:Bird:36267	1.207
Passeriformes	Pipridae	<i>Piprites chloris</i>	MSB:Bird:37326	1.224
Passeriformes	Platysteiridae	<i>Batis pririt</i>	MSB:Bird:30196	1.335
Passeriformes	Platysteiridae	<i>Batis pririt</i>	MSB:Bird:30197	1.297
Passeriformes	Ploceidae	<i>Euplectes afer</i>	MSB:Bird:30239	1.181
Passeriformes	Ploceidae	<i>Euplectes afer</i>	MSB:Bird:30240	1.203
Passeriformes	Ploceidae	<i>Euplectes albonotatus</i>	MSB:Bird:30244	1.248
Passeriformes	Ploceidae	<i>Euplectes albonotatus</i>	MSB:Bird:30245	1.201
Passeriformes	Ploceidae	<i>Euplectes ardens</i>	MSB:Bird:30235	1.114
Passeriformes	Ploceidae	<i>Euplectes ardens</i>	MSB:Bird:30236	1.118
Passeriformes	Ploceidae	<i>Euplectes orix</i>	MSB:Bird:30282	1.186

Passeriformes	Ploceidae	<i>Euplectes progne</i>	MSB:Bird:30284	1.229
Passeriformes	Ploceidae	<i>Euplectes progne</i>	MSB:Bird:30285	1.218
Passeriformes	Ploceidae	<i>Philetairus socius</i>	MSB:Bird:30232	1.499
Passeriformes	Ploceidae	<i>Philetairus socius</i>	MSB:Bird:30233	1.465
Passeriformes	Ploceidae	<i>Plocepasser mahali</i>	MSB:Bird:30230	1.282
Passeriformes	Ploceidae	<i>Plocepasser mahali</i>	MSB:Bird:30231	1.344
Passeriformes	Ploceidae	<i>Ploceus capensis</i>	MSB:Bird:30271	1.167
Passeriformes	Ploceidae	<i>Ploceus capensis</i>	MSB:Bird:30395	1.155
Passeriformes	Ploceidae	<i>Sporopipes squamifrons</i>	MSB:Bird:30248	1.381
Passeriformes	Poliopitilidae	<i>Poliopitila plumbea</i>	MSB:Bird:33721	1.246
Passeriformes	Poliopitilidae	<i>Poliopitila plumbea</i>	MSB:Bird:33824	1.256
Passeriformes	Ptiligonatidae	<i>Phainopepla nitens</i>	MSB:Bird:29255	1.826
Passeriformes	Pycnonotidae	<i>Pycnonotus nigricans</i>	MSB:Bird:30359	1.205
Passeriformes	Pycnonotidae	<i>Pycnonotus nigricans</i>	MSB:Bird:30360	1.215
Passeriformes	Stenostiridae	<i>Stenostira scita</i>	MSB:Bird:30148	1.236
Passeriformes	Stenostiridae	<i>Stenostira scita</i>	MSB:Bird:30149	1.227
Passeriformes	Sturnidae	<i>Lamprotornis nitens</i>	MSB:Bird:30100	1.167
Passeriformes	Sturnidae	<i>Lamprotornis nitens</i>	MSB:Bird:30101	1.276
Passeriformes	Sylviidae	<i>Chamaea fasciata</i>	MSB:Bird:29211	1.348
Passeriformes	Sylviidae	<i>Parisoma subcaeruleum</i>	MSB:Bird:30142	1.293
Passeriformes	Sylviidae	<i>Parisoma subcaeruleum</i>	MSB:Bird:30145	1.220
Passeriformes	Sylviidae	<i>Phylloscopus trochilus</i>	MSB:Bird:30167	1.323
Passeriformes	Sylviidae	<i>Sylvia communis</i>	MSB:Bird:30198	1.302
Passeriformes	Thamnophilidae	<i>Cercomacra serva</i>	MSB:Bird:36612	1.298
Passeriformes	Thamnophilidae	<i>Epinecrophylla spodionota</i>	MSB:Bird:36349	1.389
Passeriformes	Thamnophilidae	<i>Epinecrophylla spodionota</i>	MSB:Bird:36436	1.343
Passeriformes	Thamnophilidae	<i>Gymnophithys salvini</i>	MSB:Bird:37222	1.277
Passeriformes	Thamnophilidae	<i>Gymnophithys salvini</i>	MSB:Bird:37274	1.314
Passeriformes	Thamnophilidae	<i>Hylophylax naevius</i>	MSB:Bird:36641	1.433
Passeriformes	Thamnophilidae	<i>Hylophylax naevius</i>	MSB:Bird:36656	1.454
Passeriformes	Thamnophilidae	<i>Hypocnemis subflava</i>	MSB:Bird:27299	1.316

Passeriformes	Thamnophilidae	<i>Microrhopias quixensis</i>	MSB:Bird:36732	1.388
Passeriformes	Thamnophilidae	<i>Microrhopias quixensis</i>	MSB:Bird:36735	1.349
Passeriformes	Thamnophilidae	<i>Myrmeciza fortis</i>	MSB:Bird:37156	1.302
Passeriformes	Thamnophilidae	<i>Myrmoborus leucophrys</i>	MSB:Bird:36619	1.470
Passeriformes	Thamnophilidae	<i>Myrmoborus leucophrys</i>	MSB:Bird:36646	1.470
Passeriformes	Thamnophilidae	<i>Myrmotherula longicauda</i>	MSB:Bird:36614	1.362
Passeriformes	Thamnophilidae	<i>Myrmotherula longipennis</i>	MSB:Bird:37251	1.321
Passeriformes	Thamnophilidae	<i>Myrmotherula schisticolor</i>	MSB:Bird:36115	1.260
Passeriformes	Thamnophilidae	<i>Myrmotherula schisticolor</i>	MSB:Bird:36358	1.321
Passeriformes	Thamnophilidae	<i>Pyriglena leuconota</i>	MSB:Bird:36697	1.380
Passeriformes	Thamnophilidae	<i>Rhegmatorhina</i>	MSB:Bird:36483	1.377
		<i>melanosticta</i>		
Passeriformes	Thamnophilidae	<i>Rhegmatorhina</i>	MSB:Bird:37160	1.279
		<i>melanosticta</i>		
Passeriformes	Thamnophilidae	<i>Thamnistes anabatinus</i>	MSB:Bird:36251	1.220
Passeriformes	Thamnophilidae	<i>Thamnistes anabatinus</i>	MSB:Bird:36271	1.383
Passeriformes	Thamnophilidae	<i>Thamnophilus aethiops</i>	MSB:Bird:37334	1.338
Passeriformes	Thamnophilidae	<i>Thamnophilus bernardi</i>	MSB:Bird:34668	1.508
Passeriformes	Thamnophilidae	<i>Thamnophilus bernardi</i>	MSB:Bird:34728	1.415
Passeriformes	Thamnophilidae	<i>Thamnophilus doliatus</i>	MSB:Bird:34301	1.467
Passeriformes	Thamnophilidae	<i>Thamnophilus doliatus</i>	MSB:Bird:37242	1.443
Passeriformes	Thamnophilidae	<i>Thamnophilus murinus</i>	MSB:Bird:36433	1.447
Passeriformes	Thamnophilidae	<i>Thamnophilus palliatus</i>	MSB:Bird:36613	1.460
Passeriformes	Thamnophilidae	<i>Thamnophilus palliatus</i>	MSB:Bird:36836	1.446
Passeriformes	Thraupidae	<i>Anisognathus somptuosus</i>	MSB:Bird:36201	1.139
Passeriformes	Thraupidae	<i>Catamblyrhynchus</i>	MSB:Bird:35391	1.294
		<i>diadema</i>		
Passeriformes	Thraupidae	<i>Cissopis leverianus</i>	MSB:Bird:36364	1.254
Passeriformes	Thraupidae	<i>Coereba flaveola</i>	MSB:Bird:33687	1.493
Passeriformes	Thraupidae	<i>Conirostrum</i>	MSB:Bird:33053	1.393
		<i>ferrugineiventre</i>		

Passeriformes	Thraupidae	<i>Conirostrum</i> <i>ferrugineiventris</i>	MSB:Bird:33909	1.346
Passeriformes	Thraupidae	<i>Coryphospingus cucullatus</i>	MSB:Bird:34305	1.297
Passeriformes	Thraupidae	<i>Dacnis cayana</i>	MSB:Bird:36539	1.583
Passeriformes	Thraupidae	<i>Dacnis cayana</i>	MSB:Bird:36698	1.307
Passeriformes	Thraupidae	<i>Delothraupis</i> <i>castaneoventris</i>	MSB:Bird:33989	1.308
Passeriformes	Thraupidae	<i>Diglossa albilatera</i>	MSB:Bird:35904	1.324
Passeriformes	Thraupidae	<i>Diglossa caerulea</i>	MSB:Bird:32450	1.302
Passeriformes	Thraupidae	<i>Diglossa cyanea</i>	MSB:Bird:34429	1.250
Passeriformes	Thraupidae	<i>Diglossa cyanea</i>	MSB:Bird:34432	1.202
Passeriformes	Thraupidae	<i>Diglossa humeralis</i>	MSB:Bird:31390	1.287
Passeriformes	Thraupidae	<i>Diglossa mystacalis</i>	MSB:Bird:27018	1.173
Passeriformes	Thraupidae	<i>Diglossa sittoides</i>	MSB:Bird:34055	1.290
Passeriformes	Thraupidae	<i>Diglossa sittoides</i>	MSB:Bird:35154	1.332
Passeriformes	Thraupidae	<i>Dubusia taeniata</i>	MSB:Bird:34384	1.560
Passeriformes	Thraupidae	<i>Hemispingus atropileus</i>	MSB:Bird:34561	1.107
Passeriformes	Thraupidae	<i>Hemispingus melanotis</i>	MSB:Bird:35171	1.319
Passeriformes	Thraupidae	<i>Lanio versicolor</i>	MSB:Bird:36385	1.315
Passeriformes	Thraupidae	<i>Oryzoborus angolensis</i>	MSB:Bird:37265	1.291
Passeriformes	Thraupidae	<i>Phrygilus punensis</i>	MSB:Bird:34935	1.350
Passeriformes	Thraupidae	<i>Phrygilus punensis</i>	MSB:Bird:34949	1.377
Passeriformes	Thraupidae	<i>Piezorhina cinerea</i>	MSB:Bird:33846	1.387
Passeriformes	Thraupidae	<i>Piezorhina cinerea</i>	MSB:Bird:34708	1.430
Passeriformes	Thraupidae	<i>Poospiza alticola</i>	MSB:Bird:34932	1.276
Passeriformes	Thraupidae	<i>Poospiza alticola</i>	MSB:Bird:34973	1.305
Passeriformes	Thraupidae	<i>Poospiza caesar</i>	MSB:Bird:33104	1.417
Passeriformes	Thraupidae	<i>Poospiza caesar</i>	MSB:Bird:35848	1.412
Passeriformes	Thraupidae	<i>Poospiza rubecula</i>	MSB:Bird:34958	1.345
Passeriformes	Thraupidae	<i>Ramphocelus carbo</i>	MSB:Bird:36600	1.380
Passeriformes	Thraupidae	<i>Saltator maximus</i>	MSB:Bird:36671	1.397

Passeriformes	Thraupidae	<i>Schistochlamys melanopis</i>	MSB:Bird:34328	1.360
Passeriformes	Thraupidae	<i>Sicalis luteola</i>	MSB:Bird:34774	1.159
Passeriformes	Thraupidae	<i>Sicalis luteola</i>	MSB:Bird:36076	1.443
Passeriformes	Thraupidae	<i>Sicalis olivascens</i>	MSB:Bird:34934	1.320
Passeriformes	Thraupidae	<i>Sporophila caerulescens</i>	MSB:Bird:37247	1.232
Passeriformes	Thraupidae	<i>Sporophila caerulescens</i>	MSB:Bird:37287	1.214
Passeriformes	Thraupidae	<i>Sporophila nigricollis</i>	MSB:Bird:34315	1.360
Passeriformes	Thraupidae	<i>Sporophila peruviana</i>	MSB:Bird:34765	1.277
Passeriformes	Thraupidae	<i>Sporophila peruviana</i>	MSB:Bird:34910	1.296
Passeriformes	Thraupidae	<i>Tachyphonus rufus</i>	MSB:Bird:34320	1.407
Passeriformes	Thraupidae	<i>Tachyphonus rufus</i>	MSB:Bird:34331	1.347
Passeriformes	Thraupidae	<i>Tangara cyanicollis</i>	MSB:Bird:36322	1.325
Passeriformes	Thraupidae	<i>Tangara cyanicollis</i>	MSB:Bird:36623	1.293
Passeriformes	Thraupidae	<i>Tangara mexicana</i>	MSB:Bird:37255	1.291
Passeriformes	Thraupidae	<i>Tangara vassorii</i>	MSB:Bird:35365	1.375
Passeriformes	Thraupidae	<i>Thlypopsis ornata</i>	MSB:Bird:34831	1.340
Passeriformes	Thraupidae	<i>Thlypopsis ornata</i>	MSB:Bird:36075	1.384
Passeriformes	Thraupidae	<i>Thlypopsis ruficeps</i>	MSB:Bird:33949	1.401
Passeriformes	Thraupidae	<i>Thlypopsis ruficeps</i>	MSB:Bird:33959	1.407
Passeriformes	Thraupidae	<i>Thraupis bonariensis</i>	MSB:Bird:36048	1.274
Passeriformes	Thraupidae	<i>Thraupis episcopus</i>	MSB:Bird:33795	1.367
Passeriformes	Thraupidae	<i>Thraupis palmarum</i>	MSB:Bird:37183	1.231
Passeriformes	Thraupidae	<i>Thraupis palmarum</i>	MSB:Bird:37241	1.300
Passeriformes	Thraupidae	<i>Tiaris obscurus</i>	MSB:Bird:34717	1.298
Passeriformes	Thraupidae	<i>Xenodacnis parina</i>	MSB:Bird:35992	1.231
Passeriformes	Thraupidae	<i>Xenodacnis parina</i>	MSB:Bird:36021	1.275
Passeriformes	Thraupidae	<i>Xenospingus concolor</i>	MSB:Bird:35445	1.376
Passeriformes	Tityridae	<i>Laniocera hypopyrra</i>	MSB:Bird:36441	1.363
Passeriformes	Tityridae	<i>Pachyramphus</i> <i>polychopterus</i>	MSB:Bird:34275	1.264
Passeriformes	Tityridae	<i>Pachyramphus versicolor</i>	MSB:Bird:31874	1.285

Passeriformes	Tityridae	<i>Pachyramphus viridis</i>	MSB:Bird:36493	1.299
Passeriformes	Tityridae	<i>Schiffornis turdina</i>	MSB:Bird:36136	1.240
Passeriformes	Tityridae	<i>Schiffornis turdina</i>	MSB:Bird:36772	1.386
Passeriformes	Troglodytidae	<i>Campylorhynchus fasciatus</i>	MSB:Bird:34725	1.359
Passeriformes	Troglodytidae	<i>Campylorhynchus fasciatus</i>	MSB:Bird:35366	1.495
Passeriformes	Troglodytidae	<i>Cantorchilus superciliaris</i>	MSB:Bird:33737	1.285
Passeriformes	Troglodytidae	<i>Cantorchilus superciliaris</i>	MSB:Bird:33753	1.307
Passeriformes	Troglodytidae	<i>Cyphorhinus thoracicus</i>	MSB:Bird:36781	1.260
Passeriformes	Troglodytidae	<i>Cyphorhinus thoracicus</i>	MSB:Bird:36797	1.277
Passeriformes	Troglodytidae	<i>Pheugopedius eisenmanni</i>	MSB:Bird:34609	1.251
Passeriformes	Troglodytidae	<i>Troglodytes aedon</i>	MSB:Bird:36909	1.338
Passeriformes	Turdidae	<i>Catharus dryas</i>	MSB:Bird:36137	1.402
Passeriformes	Turdidae	<i>Catharus ustulatus</i>	MSB:Bird:35792	1.488
Passeriformes	Turdidae	<i>Turdus chiguanco</i>	MSB:Bird:35914	1.486
Passeriformes	Turdidae	<i>Turdus chiguanco</i>	MSB:Bird:36069	1.396
Passeriformes	Turdidae	<i>Turdus leucops</i>	MSB:Bird:36237	1.351
Passeriformes	Turdidae	<i>Turdus leucops</i>	MSB:Bird:36238	1.284
Passeriformes	Turdidae	<i>Turdus nigriceps</i>	MSB:Bird:36199	1.348
Passeriformes	Turdidae	<i>Turdus reevei</i>	MSB:Bird:33792	1.371
Passeriformes	Turdidae	<i>Turdus smithi</i>	MSB:Bird:30103	1.618
Passeriformes	Turdidae	<i>Turdus smithi</i>	MSB:Bird:30105	1.625
Passeriformes	Tyrannidae	<i>Anairetes agraphia</i>	MSB:Bird:34372	1.301
Passeriformes	Tyrannidae	<i>Anairetes alpinus</i>	MSB:Bird:34088	1.256
Passeriformes	Tyrannidae	<i>Anairetes alpinus</i>	MSB:Bird:34105	1.222
Passeriformes	Tyrannidae	<i>Anairetes flavirostris</i>	MSB:Bird:34056	1.330
Passeriformes	Tyrannidae	<i>Anairetes flavirostris</i>	MSB:Bird:34058	1.331
Passeriformes	Tyrannidae	<i>Anairetes flavirostris</i>	MSB:Bird:35102	1.302
Passeriformes	Tyrannidae	<i>Anairetes nigrocristatus</i>	MSB:Bird:35005	1.250
Passeriformes	Tyrannidae	<i>Anairetes nigrocristatus</i>	MSB:Bird:36072	1.297
Passeriformes	Tyrannidae	<i>Camptostoma obsoletum</i>	MSB:Bird:37109	1.199
Passeriformes	Tyrannidae	<i>Contopus cinereus</i>	MSB:Bird:33768	1.271

Passeriformes	Tyrannidae	<i>Contopus cinereus</i>	MSB:Bird:35346	1.216
Passeriformes	Tyrannidae	<i>Contopus fumigatus</i>	MSB:Bird:36304	1.128
Passeriformes	Tyrannidae	<i>Elaenia albiceps</i>	MSB:Bird:35363	1.327
Passeriformes	Tyrannidae	<i>Elaenia albiceps</i>	MSB:Bird:36047	1.312
Passeriformes	Tyrannidae	<i>Elaenia chiriquensis</i>	MSB:Bird:31843	1.246
Passeriformes	Tyrannidae	<i>Elaenia pallatangae</i>	MSB:Bird:34370	1.272
Passeriformes	Tyrannidae	<i>Elaenia pallatangae</i>	MSB:Bird:34536	1.229
Passeriformes	Tyrannidae	<i>Empidonax alnorum</i>	MSB:Bird:35775	1.213
Passeriformes	Tyrannidae	<i>Empidonax alnorum</i>	MSB:Bird:36331	1.236
Passeriformes	Tyrannidae	<i>Euscarthmus meloryphus</i>	MSB:Bird:34672	1.282
Passeriformes	Tyrannidae	<i>Euscarthmus meloryphus</i>	MSB:Bird:34752	1.360
Passeriformes	Tyrannidae	<i>Hemitriccus ruficularis</i>	MSB:Bird:36174	1.445
Passeriformes	Tyrannidae	<i>Knipolegus aterrimus</i>	MSB:Bird:35709	1.183
Passeriformes	Tyrannidae	<i>Knipolegus aterrimus</i>	MSB:Bird:35713	1.243
Passeriformes	Tyrannidae	<i>Knipolegus poecilocercus</i>	MSB:Bird:35930	1.211
Passeriformes	Tyrannidae	<i>Lathrotriccus euleri</i>	MSB:Bird:36112	1.280
Passeriformes	Tyrannidae	<i>Leptopogon superciliaris</i>	MSB:Bird:36786	1.176
Passeriformes	Tyrannidae	<i>Leptopogon superciliaris</i>	MSB:Bird:36807	1.232
Passeriformes	Tyrannidae	<i>Lophotriccus eulophotes</i>	MSB:Bird:37200	1.190
Passeriformes	Tyrannidae	<i>Lophotriccus pileatus</i>	MSB:Bird:36788	1.126
Passeriformes	Tyrannidae	<i>Mionectes macconnelli</i>	MSB:Bird:37121	1.180
Passeriformes	Tyrannidae	<i>Mionectes macconnelli</i>	MSB:Bird:37207	1.233
Passeriformes	Tyrannidae	<i>Mionectes macconnelli</i>	MSB:Bird:37285	1.210
Passeriformes	Tyrannidae	<i>Mionectes oleagineus</i>	MSB:Bird:37139	1.125
Passeriformes	Tyrannidae	<i>Mionectes olivaceus</i>	MSB:Bird:36629	1.326
Passeriformes	Tyrannidae	<i>Mionectes olivaceus</i>	MSB:Bird:36650	1.274
Passeriformes	Tyrannidae	<i>Mionectes olivaceus</i>	MSB:Bird:36708	1.314
Passeriformes	Tyrannidae	<i>Mionectes striaticollis</i>	MSB:Bird:36273	1.321
Passeriformes	Tyrannidae	<i>Mionectes striaticollis</i>	MSB:Bird:36744	1.329
Passeriformes	Tyrannidae	<i>Muscigralla brevicauda</i>	MSB:Bird:34214	1.218
Passeriformes	Tyrannidae	<i>Muscigralla brevicauda</i>	MSB:Bird:34716	1.230

Passeriformes	Tyrannidae	<i>Muscisaxicola fluviatilis</i>	MSB:Bird:36748	1.252
Passeriformes	Tyrannidae	<i>Muscisaxicola fluviatilis</i>	MSB:Bird:36776	1.192
Passeriformes	Tyrannidae	<i>Myiarchus tuberculifer</i>	MSB:Bird:35261	1.230
Passeriformes	Tyrannidae	<i>Myiobius villosus</i>	MSB:Bird:36838	1.203
Passeriformes	Tyrannidae	<i>Myiodynastes bairdii</i>	MSB:Bird:33774	1.265
Passeriformes	Tyrannidae	<i>Myiodynastes bairdii</i>	MSB:Bird:34800	1.286
Passeriformes	Tyrannidae	<i>Myiodynastes maculatus</i>	MSB:Bird:34312	1.307
Passeriformes	Tyrannidae	<i>Myiophobus fasciatus</i>	MSB:Bird:36677	1.285
Passeriformes	Tyrannidae	<i>Myiophobus fasciatus</i>	MSB:Bird:36706	1.264
Passeriformes	Tyrannidae	<i>Myiozetetes similis</i>	MSB:Bird:37297	1.338
Passeriformes	Tyrannidae	<i>Ochthoeca frontalis</i>	MSB:Bird:33980	1.320
Passeriformes	Tyrannidae	<i>Ochthoeca frontalis</i>	MSB:Bird:34001	1.225
Passeriformes	Tyrannidae	<i>Ochthoeca fumicolor</i>	MSB:Bird:34010	1.289
Passeriformes	Tyrannidae	<i>Ochthoeca jelskii</i>	MSB:Bird:35116	1.318
Passeriformes	Tyrannidae	<i>Ochthoeca jelskii</i>	MSB:Bird:35374	1.309
Passeriformes	Tyrannidae	<i>Ochthoeca oenanthoides</i>	MSB:Bird:34130	1.260
Passeriformes	Tyrannidae	<i>Ochthoeca oenanthoides</i>	MSB:Bird:34189	1.311
Passeriformes	Tyrannidae	<i>Ochthoeca piurae</i>	MSB:Bird:35294	1.332
Passeriformes	Tyrannidae	<i>Ochthoeca piurae</i>	MSB:Bird:35431	1.300
Passeriformes	Tyrannidae	<i>Onychorhynchus coronatus</i>	MSB:Bird:37214	1.137
Passeriformes	Tyrannidae	<i>Phaeomyias murina</i>	MSB:Bird:33676	1.265
Passeriformes	Tyrannidae	<i>Phaeomyias murina</i>	MSB:Bird:33767	1.293
Passeriformes	Tyrannidae	<i>Phaeomyias murina</i>	MSB:Bird:34754	1.299
Passeriformes	Tyrannidae	<i>Phaeomyias murina</i>	MSB:Bird:35328	1.319
Passeriformes	Tyrannidae	<i>Phyllomyias uropygialis</i>	MSB:Bird:35146	1.329
Passeriformes	Tyrannidae	<i>Platyrinchus flavigularis</i>	MSB:Bird:36363	1.144
Passeriformes	Tyrannidae	<i>Platyrinchus platyrhynchos</i>	MSB:Bird:37291	1.074
Passeriformes	Tyrannidae	<i>Platyrinchus platyrhynchos</i>	MSB:Bird:37292	1.190
Passeriformes	Tyrannidae	<i>Polioxolmis rufipennis</i>	MSB:Bird:34169	1.281
Passeriformes	Tyrannidae	<i>Polioxolmis rufipennis</i>	MSB:Bird:35995	1.201
Passeriformes	Tyrannidae	<i>Pseudotriccus ruficeps</i>	MSB:Bird:32453	1.220

Passeriformes	Tyrannidae	<i>Sayornis nigricans</i>	MSB:Bird:35894	1.260
Passeriformes	Tyrannidae	<i>Tolmomyias poliocephalus</i>	MSB:Bird:36707	1.166
Passeriformes	Tyrannidae	<i>Tyrannulus elatus</i>	MSB:Bird:37316	1.462
Passeriformes	Tyrannidae	<i>Tyrannus melancholicus</i>	MSB:Bird:34677	1.298
Passeriformes	Viduidae	<i>Vidua chalybeata</i>	MSB:Bird:30286	1.184
Passeriformes	Viduidae	<i>Vidua chalybeata</i>	MSB:Bird:30287	1.141
Passeriformes	Viduidae	<i>Vidua macroura</i>	MSB:Bird:30254	1.080
Passeriformes	Viduidae	<i>Vidua paradisaea</i>	MSB:Bird:30256	1.166
Passeriformes	Viduidae	<i>Vidua paradisaea</i>	MSB:Bird:30257	1.186
Passeriformes	Vireonidae	<i>Cyclarhis gujanensis</i>	MSB:Bird:35149	1.415
Passeriformes	Vireonidae	<i>Hylophilus ochraceiceps</i>	MSB:Bird:37147	1.241
Passeriformes	Vireonidae	<i>Hylophilus ochraceiceps</i>	MSB:Bird:37148	1.269
Passeriformes	Vireonidae	<i>Vireo olivaceus</i>	MSB:Bird:36827	1.236
Passeriformes	Zosteropidae	<i>Zosterops pallidus</i>	MSB:Bird:30217	1.351
Piciformes	Bucconidae	<i>Chelidoptera tenebrosa</i>	MSB:Bird:37070	1.304
Piciformes	Bucconidae	<i>Chelidoptera tenebrosa</i>	MSB:Bird:37339	1.261
Piciformes	Bucconidae	<i>Malacoptila fulvogularis</i>	MSB:Bird:36774	1.172
Piciformes	Bucconidae	<i>Monasa morphoeus</i>	MSB:Bird:36923	1.238
Piciformes	Bucconidae	<i>Nonnula ruficapilla</i>	MSB:Bird:36465	1.107
Piciformes	Bucconidae	<i>Nonnula ruficapilla</i>	MSB:Bird:36503	1.115
Piciformes	Bucconidae	<i>Nystalus chacuru</i>	MSB:Bird:35769	1.244
Piciformes	Bucconidae	<i>Nystalus chacuru</i>	MSB:Bird:35770	1.283
Piciformes	Bucconidae	<i>Nystalus chacuru</i>	MSB:Bird:35786	1.263
Piciformes	Capitonidae	<i>Capito auratus</i>	MSB:Bird:36367	1.229
Piciformes	Capitonidae	<i>Capito auratus</i>	MSB:Bird:37169	1.593
Piciformes	Capitonidae	<i>Capito auratus</i>	MSB:Bird:37235	1.434
Piciformes	Capitonidae	<i>Eubucco richardsoni</i>	MSB:Bird:36916	1.620
Piciformes	Capitonidae	<i>Eubucco versicolor</i>	MSB:Bird:36204	1.599
Piciformes	Capitonidae	<i>Eubucco versicolor</i>	MSB:Bird:36253	1.637
Piciformes	Capitonidae	<i>Eubucco versicolor</i>	MSB:Bird:36661	1.550
Piciformes	Galbulidae	<i>Galbula cyanescens</i>	MSB:Bird:27887	1.131

Piciformes	Galbulidae	<i>Galbula cyanescens</i>	MSB:Bird:36611	1.100
Piciformes	Galbulidae	<i>Galbula cyanescens</i>	MSB:Bird:36773	1.157
Piciformes	Galbulidae	<i>Galbula cyanescens</i>	MSB:Bird:36790	1.126
Piciformes	Indicatoridae	<i>Indicator minor</i>	MSB:Bird:30060	1.335
Piciformes	Indicatoridae	<i>Indicator minor</i>	FMNH MLW3653	1.406
Piciformes	Indicatoridae	<i>Indicator minor</i>	MSB:Bird:30058	1.389
Piciformes	Indicatoridae	<i>Indicator minor</i>	MSB:Bird:30059	1.369
Piciformes	Indicatoridae	<i>Indicator minor</i>	MSB:Bird:30061	1.352
Piciformes	Indicatoridae	<i>Indicator variegatus</i>	FMNH MLW3882	2.098
Piciformes	Indicatoridae	<i>Indicator variegatus</i>	FMNH MLW4130	1.997
Piciformes	Lybiidae	<i>Lybius torquatus</i>	FMNH MLW3421	1.753
Piciformes	Lybiidae	<i>Trachyphonus vaillantii</i>	FMNH MLW3406	1.711
Piciformes	Lybiidae	<i>Trachyphonus vaillantii</i>	MSB:Bird:30073	1.740
Piciformes	Lybiidae	<i>Trachyphonus vaillantii</i>	MSB:Bird:30078	1.604
Piciformes	Lybiidae	<i>Tricholaema leucomelas</i>	MSB:Bird:30331	1.615
Piciformes	Lybiidae	<i>Tricholaema leucomelas</i>	MSB:Bird:30332	1.591
Piciformes	Lybiidae	<i>Tricholaema leucomelas</i>	MSB:Bird:30333	1.548
Piciformes	Picidae	<i>Campephilus</i> <i>haematogaster</i>	MSB:Bird:36897	1.508
Piciformes	Picidae	<i>Campephilus rubricollis</i>	MSB:Bird:37087	1.389
Piciformes	Picidae	<i>Campephilus rubricollis</i>	MSB:Bird:37314	1.394
Piciformes	Picidae	<i>Campethera abingoni</i>	FMNH MLW3767	1.664
Piciformes	Picidae	<i>Campethera abingoni</i>	MSB:Bird:30075	1.560
Piciformes	Picidae	<i>Campethera abingoni</i>	MSB:Bird:30076	1.472
Piciformes	Picidae	<i>Colaptes atricollis</i>	MSB:Bird:35053	1.506
Piciformes	Picidae	<i>Colaptes rivolii</i>	MSB:Bird:33958	1.542
Piciformes	Picidae	<i>Colaptes rubiginosus</i>	MSB:Bird:33769	1.521
Piciformes	Picidae	<i>Colaptes rubiginosus</i>	MSB:Bird:33789	1.549
Piciformes	Picidae	<i>Colaptes rubiginosus</i>	MSB:Bird:33840	1.507
Piciformes	Picidae	<i>Colaptes rubiginosus</i>	MSB:Bird:36155	1.573
Piciformes	Picidae	<i>Colaptes rupicola</i>	MSB:Bird:34196	1.479

Piciformes	Picidae	<i>Dryocopus lineatus</i>	MSB:Bird:37181	1.665
Piciformes	Picidae	<i>Jynx ruficollis</i>	MSB:Bird:30350	1.312
Piciformes	Picidae	<i>Melanerpes cruentatus</i>	MSB:Bird:36247	1.623
Piciformes	Picidae	<i>Melanerpes cruentatus</i>	MSB:Bird:36356	1.634
Piciformes	Picidae	<i>Melanerpes formicivorus</i>	MSB:Bird:30028	1.686
Piciformes	Picidae	<i>Picoides dorsalis</i>	MSB:Bird:30035	1.328
Piciformes	Picidae	<i>Picoides fumigatus</i>	MSB:Bird:34981	1.471
Piciformes	Picidae	<i>Picoides fumigatus</i>	MSB:Bird:35124	1.480
Piciformes	Picidae	<i>Picoides nuttallii</i>	MSB:Bird:29213	1.509
Piciformes	Picidae	<i>Picoides villosus</i>	MSB:Bird:30517	1.378
Piciformes	Picidae	<i>Picumnus subtilis</i>	MSB:Bird:36621	1.564
Piciformes	Picidae	<i>Picumnus subtilis</i>	MSB:Bird:36642	1.605
Piciformes	Picidae	<i>Picumnus subtilis</i>	MSB:Bird:36643	1.570
Piciformes	Picidae	<i>Picumnus subtilis</i>	MSB:Bird:36871	1.614
Piciformes	Picidae	<i>Veniliornis callonotus</i>	MSB:Bird:33682	1.458
Piciformes	Picidae	<i>Veniliornis callonotus</i>	MSB:Bird:33698	1.503
Piciformes	Picidae	<i>Veniliornis callonotus</i>	MSB:Bird:33716	1.531
Piciformes	Picidae	<i>Veniliornis callonotus</i>	MSB:Bird:33730	1.455
Piciformes	Ramphastidae	<i>Aulacorhynchus derbianus</i>	MSB:Bird:36156	1.687
Piciformes	Ramphastidae	<i>Aulacorhynchus prasinus</i>	MSB:Bird:36799	1.672
Piciformes	Ramphastidae	<i>Pteroglossus azara</i>	MSB:Bird:36496	1.447
Piciformes	Ramphastidae	<i>Pteroglossus azara</i>	MSB:Bird:36501	1.542
Piciformes	Ramphastidae	<i>Pteroglossus beauharnaesii</i>	MSB:Bird:37298	1.433
Piciformes	Ramphastidae	<i>Pteroglossus inscriptus</i>	MSB:Bird:37338	1.564
Piciformes	Ramphastidae	<i>Ramphastos tucanus</i>	MSB:Bird:37102	1.573
Piciformes	Ramphastidae	<i>Selenidera reinwardtii</i>	MSB:Bird:36295	1.588
Piciformes	Ramphastidae	<i>Selenidera reinwardtii</i>	MSB:Bird:37046	1.598
Piciformes	Ramphastidae	<i>Selenidera reinwardtii</i>	MSB:Bird:37303	1.515
Piciformes	Ramphastidae	<i>Selenidera reinwardtii</i>	MSB:Bird:37304	1.531
Podicipediformes	Podicipedidae	<i>Tachybaptus ruficollis</i>	MSB:Bird:30041	1.585
Psittaciformes	Psittacidae	<i>Aratinga leucophthalma</i>	MSB:Bird:37307	1.466

Psittaciformes	Psittacidae	<i>Aratinga mitrata</i>	MSB:Bird:35753	1.533
Psittaciformes	Psittacidae	<i>Bolborhynchus lineola</i>	MSB:Bird:34605	1.434
Psittaciformes	Psittacidae	<i>Bolborhynchus lineola</i>	MSB:Bird:34606	1.411
Psittaciformes	Psittacidae	<i>Bolborhynchus orbygnesi</i>	MSB:Bird:35320	1.515
Psittaciformes	Psittacidae	<i>Brotogeris cyanoptera</i>	MSB:Bird:36482	1.334
Psittaciformes	Psittacidae	<i>Forpus coelestis</i>	MSB:Bird:33690	1.519
Psittaciformes	Psittacidae	<i>Forpus coelestis</i>	MSB:Bird:33748	1.560
Psittaciformes	Psittacidae	<i>Pyrrhura roseifrons</i>	MSB:Bird:36342	1.405
Psittaciformes	Psittacidae	<i>Pyrrhura roseifrons</i>	MSB:Bird:36492	1.384
Strigiformes	Strigidae	<i>Glaucidium peruanum</i>	MSB:Bird:35444	1.551
Strigiformes	Strigidae	<i>Glaucidium peruanum</i>	MSB:Bird:35487	1.547
Strigiformes	Strigidae	<i>Megascops ingens</i>	MSB:Bird:32525	1.655
Strigiformes	Strigidae	<i>Megascops koepckeae</i>	MSB:Bird:35144	1.542
Strigiformes	Strigidae	<i>Megascops koepckeae</i>	MSB:Bird:35304	1.530
Tinamiformes	Tinamidae	<i>Crypturellus obsoletus</i>	MSB:Bird:37037	1.350
Tinamiformes	Tinamidae	<i>Eudromia elegans</i>	MSB:Bird:28915	1.241
Trogoniformes	Trogonidae	<i>Trogon collaris</i>	MSB:Bird:36263	1.356
Trogoniformes	Trogonidae	<i>Trogon collaris</i>	MSB:Bird:37319	1.465

Table S2: Single variable models with genome size as the dependent variable.

model type	predictor variable	adj. R^2	df	p-value
PGLS	flight muscles	0.05	287	< 0.001
PGLS	heart index	0.049	287	< 0.001
PGLS	body mass	0.015	287	0.019
PGLS	wing loading	0.007	191	0.013
PGLS	hand-wing index	0.005	191	0.78
regression	flight muscles	0.12	287	< 0.001
regression	heart index	0.25	287	< 0.001
regression	body mass	0.33	287	< 0.001
regression	wing loading	0.25	191	< 0.001
regression	hand-wing index	0.03	191	0.01

Table S3: Sample sizes (number of species), means (of species means), 95% confidence intervals (of taxon means) and coefficients of variation for genome sizes of 76 families.

order	family	N	mean	95% CI	coefficient of variation
Tinamiformes	Tinamidae	2	1.30	(0.60, 1.99)	0.06
Galliformes	Phasianidae	3	1.22	(1.18, 1.26)	0.01
Podicipediformes	Podicipedidae	1	1.58	-	-
Columbiformes	Columbidae	7	1.43	(1.38, 1.48)	0.04
Cuculiformes	Cuculidae	5	1.40	(1.31, 1.50)	0.05
Caprimulgiformes	Caprimulgidae	4	1.37	(1.14, 1.60)	0.11
Apodiformes	-	47	1.18	(1.17, 1.20)	0.05
Apodiformes	Apodidae	4	1.23	(1.05, 1.40)	0.09
Apodiformes	Trochilidae	43	1.18	(1.16, 1.19)	0.04
Strigiformes	Strigidae	3	1.58	(1.42, 	0.04

1.74)					
Pelecaniformes	Scopidae	1	1.35	-	-
Pelecaniformes	Threskiornithidae	1	1.47	-	-
Charadriiformes	Charadriidae	1	1.67	-	-
Charadriiformes	Turnicidae	1	1.26	-	-
Coliiformes	Coliidae	2	1.50	(1.12,	0.03
1.87)					
Accipitriformes	Accipitridae	1	1.55	-	-
Falconiformes	Falconidae	2	1.50	(0.60,	0.07
2.4)					
Trogoniformes	Trogonidae	1	1.41	-	-
Coraciiformes	-	9	1.37	(1.26,	0.10
1.48)					
Coraciiformes	Phoeniculidae	2	1.22	(0.01,	0.11
2.43)					
Coraciiformes	Upupidae	1	1.28	-	-
Coraciiformes	Coraciidae	1	1.28	-	-
Coraciiformes	Meropidae	2	1.35	(1.03,	0.03
1.66)					
Coraciiformes	Alcedinidae	1	1.58	-	-
Coraciiformes	Momotidae	2	1.51	(1.38,	0.01
1.64)					
Piciformes	-	38	1.50	(1.43,	0.12

				1.56)	
Piciformes	Lybiidae	3	1.67	(1.46, 1.88)	0.05
Piciformes	Bucconidae	5	1.21	(1.13, 1.30)	0.06
Piciformes	Galbulidae	1	1.13	-	-
Piciformes	Capitonidae	3	1.54	(1.27, 1.82)	0.07
Piciformes	Ramphastidae	7	1.57	(1.49, 1.65)	0.06
Piciformes	Picidae	17	1.51	(1.45, 1.56)	0.07
Piciformes	Indicatoridae	2	1.71	(-2.53, 5.96)	0.28
Psittaciformes	Psittacidae	7	1.46	(1.39, 1.53)	0.05
Passeriformes	-	286	1.31	(1.30, 1.32)	0.08
Passeriformes	Thamnophilidae	21	1.36	(1.34, 1.40)	0.05
Passeriformes	Furnariidae	30	1.29	(1.26, 1.32)	0.06
Passeriformes	Formicariidae	1	1.28	-	-

Passeriformes	Grallariidae	3	1.37	(1.18, 1.55)	0.05
Passeriformes	Tyrannidae	47	1.25	(1.23, 1.28)	0.06
Passeriformes	Conopophagidae	1	1.45	-	-
Passeriformes	Pipridae	6	1.23	(1.20, 1.25)	0.02
Passeriformes	Cotingidae	7	1.42	(1.29, 1.56)	0.10
Passeriformes	Tityridae	5	1.30	(1.26, 1.35)	0.03
Passeriformes	Hirundinidae	5	1.40	(1.35, 1.45)	0.03
Passeriformes	Vireonidae	3	1.30	(1.06, 1.55)	0.08
Passeriformes	Laniidae	3	1.22	(1.11, 1.34)	0.04
Passeriformes	Malaconotidae	3	1.22	(1.07, 1.37)	0.05
Passeriformes	Ptiliognatidae	1	1.83	-	-
Passeriformes	Paridae	2	1.26	(0.58, 1.94)	0.06
Passeriformes	Turdidae	7	1.43	(1.33, 1.53)	0.07

				1.52)	
Passeriformes	Cinclidae	1	1.28	-	-
Passeriformes	Troglodytidae	5	1.32	(1.23,	0.05
				1.40)	
Passeriformes	Mimidae	1	1.32	-	-
Passeriformes	Poliophtilidae	1	1.25	-	-
Passeriformes	Cisticolidae	8	1.17	(1.11,	0.06
				1.23)	
Passeriformes	Alaudidae	1	1.25	-	-
Passeriformes	Muscicapidae	8	1.32	(1.24,	0.07
				1.38)	
Passeriformes	Stenostiridae	1	1.23	-	-
Passeriformes	Platysteiridae	1	1.32	-	-
Passeriformes	Sylviidae	4	1.31	(1.19,	0.03
				1.42)	
Passeriformes	Macrosphenidae	1	1.31	-	-
Passeriformes	Acrocephalidae	2	1.31	(1.03,	0.02
				1.59)	
Passeriformes	Motacillidae	5	1.22	(1.09,	0.09
				1.35)	
Passeriformes	Ploceidae	9	1.25	(1.16,	0.09
				1.34)	
Passeriformes	Dicruridae	1	1.13	-	-

Passeriformes	Pycnonotidae	1	1.21	-	-
Passeriformes	Sturnidae	1	1.22	-	-
Passeriformes	Zosteropidae	1	1.35	-	-
Passeriformes	Passeridae	2	1.31	(1.31, 1.32)	0.00
Passeriformes	Viduidae	3	1.14	(1.01, 1.27)	0.05
Passeriformes	Estrildidae	8	1.33	(1.22, 1.44)	0.10
Passeriformes	Parulidae	7	1.43	(1.39, 1.47)	0.03
Passeriformes	Thraupidae	44	1.32	(1.30, 1.35)	0.06
Passeriformes	Cardinalidae	3	1.42	(1.26, 1.58)	0.05
Passeriformes	Passerellidae	11	1.42	(1.33, 1.51)	0.09
Passeriformes	Fringillidae	5	1.34	(1.20, 1.48)	0.08
Passeriformes	Emberizidae	2	1.32	(0.51, 2.12)	0.07
Passeriformes	Icteridae	4	1.40	(1.26, 1.55)	0.07

Appendix 2: Supplementary Materials for Chapter 2

Supplemental Materials and Methods

Data collection

We collected bird specimens using standard museum methods (Wright and Steadman 2012; Wright et al. 2014). We weighed each bird and extracted and weighed the fresh pectoralis major and supracoracoideus muscles. Relative flight muscle size was calculated by dividing total flight muscle mass by body mass, as flight muscle mass scales isometrically with body mass. Species values were obtained by taking the mean of the average male measurement and average female measurement of each species. Data come from specimens at the Museum of Southwestern Biology (University of New Mexico, USA), Centro de Ornitología y Biodiversidad (Lima, Peru), and Florida Museum of Natural History (University of Florida, USA).

To increase sampling, we used skeletal specimens from historic collections, focusing on the following well-represented taxa: Trochilidae; *Macropygia*, *Ducula*, *Ptilinopus*, *Columbina*, and *Zenaida aurita* (Columbidae); Alcedinidae; Zosteropidae; *Rhipidura* (Rhipiduridae); Meliphagidae; Monarchidae; *Pachycephala* (Pachycephalidae); *Coereba flaveola*, *Tiaris*, and *Loxigilla* (Thraupidae). The flight muscles attach to the sternal keel, and keel size is closely related to flight muscle size. A single measurement, the diagonal length of the keel, which encompasses both length and depth, was the best predictor of flight muscle size and correlates strongly with flight muscle mass both within and among species (see “Supplementary Text” for details). We measured all available skeletal specimens of our focal island taxa at five natural history museums with large avian skeletal collections (see data.csv file for complete list of all

specimens measured and associated data). One person (N.A.W.) made all of the following measurements from each skeletal specimen: bill length, width, and depth; keel diagonal length and keel depth; and the lengths of the cranium, sternum, coracoid, humerus, ulna, carpometacarpus, femur, tibiotarsus, tarsometatarsus. Specimens missing any of the following elements were excluded from analyses: sternal keel, coracoid, humerus, femur, and tarsometatarsus.

Data on area and landbird species richness were collected for each island from which we had bird skeletal measurements. Species richness numbers were calculated from species accounts in the literature (duPont 1976; ffrench 1991; Raffaele et al. 1998; Kennedy et al. 2000; Steadman 2006) and species checklists (Lepage 2014) and included regularly occurring species whether resident or migrant, but excluded vagrants and rarities.

Analyses

We analyzed three distinct datasets. Analysis 1: species means of relative flight muscle mass; Analysis 2: means of skeletal characters for each island population (i.e., one value for each species on each island); and Analysis 3: skeletal measurements of individuals.

Analysis 1: We tested whether island-restricted species have evolved smaller flight muscles than their continental relatives by conducting phylogenetic generalized linear models (PGLS) in R with packages *ape* and *nlme* (Paradis et al. 2004; Pinheiro et al. 2012; R Core Team 2012) using a phylogenetic tree for birds (Jetz et al. 2012) and species averages of relative flight muscle sizes. Species found on both continents and

islands (including migrants) were coded as continental. We coded species as “island-restricted” if they were not regularly found on any continent. Because some large islands are continent-like in their ecology (e.g., New Guinea has roughly the same landbird species richness as Australia), we considered only species endemic to islands smaller than 200,000km² to be “island-restricted”. We restricted analyses to landbirds only (i.e., excluded ducks, seabirds, shorebirds, and grebes). Our dataset included average relative flight muscle sizes for 868 species. Only 59 of these are restricted to islands, and only 38 of them are restricted to islands smaller than 200,000km². We determined which model among null, Brownian motion, Ornstein-Uhlenbeck, and Pagel’s lambda models best described the flight muscle data using AIC. We used this best model correlation structure in PGLS analyses.

Analyses 2 and 3: To test whether flight muscle size and leg lengths are related to island species richness or area, we analyzed skeletal measurements in a variety of ways. First, we used principal component analysis on length measurements of the coracoid, humerus, femur, and tarsometatarsus to correct for body size, as the first principal component (PC1) of this analysis included all four variables loading roughly equally and in the same direction. We used the residuals of a linear model of the skeletal element of interest (i.e., keel length and tarsometatarsus length) by PC1 as a body size-corrected estimate of the character. All results presented are these body size-corrected estimates rather than raw values. Because in most cases keel length and leg length were evolving in concert and were strongly negatively correlated, we created a shape index to characterize small flight muscles and long legs. This shape index was the second principal component (PC2) from a principal component analysis on keel length and leg length measurements.

Both keel and leg length loaded equally and in the same direction in PC1, and in opposite directions in PC2. PC2 explained 25% of the variation when analyzed across the entire dataset.

Analysis 2A: We conducted phylogenetic generalized least squares linear model (PGLS) analysis on the entire skeletal dataset, with island population as the unit for analysis, and island population means calculated from individual-level data. The PCA was conducted across all individuals, with PC1 and residual values averaged for each island population. This analysis required a phylogenetic tree that included relationships among island populations. Therefore, we patched hypothesized relationships among island populations into a species-level tree from Jetz et al. (2012), largely derived in its major clades from Hackett et al. (Hackett et al. 2008). We used published phylogeographic studies (Bellemain et al. 2008; Sanchez-Gonzalez and Moyle 2011; Andersen 2013; Andersen et al. 2013; Andersen et al. 2014; Hosner et al. 2014; Andersen et al. 2015) as the basis for hypothesized relationships among island populations. For taxa without published phylogeographic studies, we hypothesized relationships based on subspecies differentiation, relationships among populations of similar species on the same islands, and geographic proximity of islands.

While conducting phylogenetic comparative analyses across populations rather than species is not ideal, there is not a feasible alternative. We note that species delimitations are currently under revision for many of our island taxa (Andersen et al. 2013; Andersen et al. 2014; Andersen et al. 2015). These recent studies suggest that many of our island “populations” probably represent reproductively isolated, independent monophyletic lineages, considered by most experts to be separate species.

Phylogeographic work is ongoing and likely to result in more such cases. Where island populations have not yet reached biological species status, these populations may still be isolated from other populations and experiencing reduced to no gene flow with other island populations. Thus we treat each island population as an independent lineage for phylogenetic comparative analyses.

Analysis 2B: We conducted linear regression analyses with the character of interest by species richness and island area, respectively, on population-level data. We used the same methods as in analysis 2 for calculating island population means, and conducted non-phylogenetic linear regression analyses on these data.

Analysis 3A: We conducted linear regression analyses with the character of interest by species richness and island area, respectively. We analyzed each taxon independently, with the individual specimen as the unit of analysis. We conducted PCAs separately for each taxon of interest. Sex and species were included as covariates in multiple regressions. We report the full model for each morphological character by species richness in Table S6.

Analysis 3B: To test predictions of the island rule, we examined how the body size of the focal taxon affected the relationship between body size and species richness and island area, respectively. For each genus with sample $n \geq 10$ and island populations $n > 3$, we performed a linear regression between body size (PC1) and species richness. We regressed the coefficient of the relationship between body size and species richness against mean body size of the genus. We repeated the analysis with the slope set to 0 for taxa in which the linear regression of body size \sim species richness was not statistically significant at $p < 0.05$. We performed this analysis for all taxa together, and also for

Columbidae and Passeriformes separately. If the taxa in our study follow the island rule, we would expect the relationship to be positive: small-bodied species should have negative relationships between island species richness and body size, whereas large-bodied taxa should become smaller as island species richness decreases (figure S1).

Supplementary Text

Relationship between keel length and flight muscle mass

Individual-level analyses: We reduced our dataset to individual specimens for which we had both flight muscle masses and skeletal measurements. Keel length was strongly correlated with flight muscle mass across all individuals ($p < 0.001$, adj. $R^2 = 0.81$, df: 1 and 165). We conducted a PCA across this entire dataset to correct for body size, as described above. Body size-corrected keel length was positively correlated with relative flight muscle size ($p < 0.001$, adj. $R^2 = 0.58$, df: 1 and 165).

We then focused on within-lineage relationships between keel length and flight muscle size. In *Coereba flaveola* body size-corrected keel length was positively correlated with relative flight muscle size ($p = 0.004$, adj. $R^2 = 0.22$, df: 1 and 30; results were nearly identical when correcting for body size using PC1 from the PCA run above, or when a new PCA was conducted using only *Coereba flaveola* samples). Likewise, in the pigeon *Macropygia mackinlayi* keel length was positively correlated with flight muscle size (body size-corrected: $p = 0.0029$, adj. $R^2 = 0.61$, df: 1 and 9; raw length and mass values, uncorrected for body size: $p = 0.0049$, adj. $R^2 = 0.56$). These were the only two species for which we had at least 10 samples with both skeletal and flight muscle mass data. Looking across individuals in the fruit-dove genus *Ptilinopus*, we also found

that keel length was positively correlated with flight muscle size (body size-corrected: $p < 0.001$, adj. $R^2 = 0.63$, df: 1 and 15; not body size-corrected: $p < 0.001$, adj. $R^2 = 0.85$). Similar results were found for the *Zosterops* white-eyes (body size-corrected: $p = 0.0019$, adj. $R^2 = 0.50$, df: 1 and 13; not body size-corrected: $p < 0.001$, adj. $R^2 = 0.63$) and the *Rhipidura* fantails (body size-corrected: $p = 0.14$, adj. $R^2 = 0.12$, df: 1 and 11; not body size-corrected: $p < 0.001$, adj. $R^2 = 0.90$).

Species average analyses: We calculated species averages of the skeletal measurements, including PC1 and body size-corrected characters, and combined this dataset with the dataset on species averages of flight muscle masses. We used phylogenetic generalized linear models (PGLS) as described in the methods above to test how keel length and flight muscle size were related across species in a phylogenetic context. Species averages of body size-corrected keel length were positively correlated with relative flight muscle sizes (PGLS: $p < 0.001$, $R^2 = 0.47$, df: 41). Likewise, uncorrected keel length was strongly correlated with flight muscle mass (PGLS: $p < 0.001$, $R^2 = 0.65$, df: 41).

While skeletal proxies for flight muscle size such as keel length are highly correlated with flight muscle mass, measurements taken on skeletal specimens are more precise and accurate. Our flight muscle data were collected over the span of a decade by dozens of specimen preparators, often in less than ideal field conditions, whereas one investigator (N.A.W.) made all skeletal measurements in the comfort of museum collections. Additionally, flight muscle mass varies within an individual in response to body condition, migration, season, and breeding, but skeletal structures are less labile.

These naturally occurring variations in flight muscle mass along with measurement error likely account for much of the variation left unexplained by keel length.

Evolution toward flightlessness in island birds

Our findings that birds evolve smaller flight muscles and longer legs on smaller, more species-poor islands are robust to analytic method, taxonomic scale, and island system. Our data come from populations on oceanic and continental islands in the Pacific and Caribbean. They include Old World kingfishers, Old World and New World doves and pigeons, hummingbirds (New World-restricted), and both Old and New World families of passerines. We reach the same conclusions whether testing the question across lineages in a phylogenetic comparative framework or when focusing on within-species or within-genera comparisons and whether we use island population means or individual values as the units of analysis (Tables S2-S4).

Analysis 1: Pagel's lambda correlation structure best described the flight muscle mass data. Across all landbirds, island-restricted species had smaller flight muscles than their continental relatives (PGLS: $p < 0.001$; df: 866). Relative flight muscle size is mechanistically tied to flight style and body plan, and displays high phylogenetic signal (Pagel's $\lambda = 0.89$). Family alone explains 71% of the variation in relative flight muscle size across birds ($p < 0.001$; df: 104 and 847). We focused on family Columbidae (pigeons and doves), for which we had data on 59 species, 8 of which are restricted to islands smaller than 200,000km² (13.6%). This was the only family for which we had data on >4 small-island-restricted species and >4 continental species. Within Columbidae, relative flight muscle mass exhibited little phylogenetic signal (Pagel's $\lambda = 0.23$) and there was

little difference between the fit of the null model and Pagel's lambda correlation structure (AIC -222.6 and -222.0, respectively). Island-restricted columbids had smaller relative flight muscles than their continental relatives in both PGLS ($p < 0.001$, df: 57) and non-phylogenetic linear regression ($p < 0.001$, adj. $R^2 = 0.26$, df: 57).

Analysis 2: Pagel's lambda correlation structure best described the keel length, tarsometatarsus length, and air-ground index data, with each exhibiting high phylogenetic signal (Pagel's $\lambda = 0.95, 0.98$, and 0.97 , respectively). Body size-corrected keel length and the air-ground index correlated positively with island species richness and island area, while body size-corrected tarsometatarsus length correlated negatively with island species richness and island area. This was the case for phylogenetic generalized linear models and non-phylogenetic linear regressions of island population means (Tables 1, S2, S3).

Testing the island rule

Analysis 3B: There was no significant relationship between body size and the direction of body size change on islands (non-significant slopes set to 0: all taxa: $p = 0.65$, $R^2 = 0.01$, df: 1 and 17; Columbidae: $p = 0.73$, $R^2 = 0.03$, df: 1 and 4; Passeriformes: $p = 0.24$, $R^2 = 0.19$, df: 1 and 7; non-significant slopes included: all taxa: $p = 0.52$, $R^2 = 0.02$, df: 1 and 17; Columbidae: $p = 0.74$, $R^2 = 0.03$, df: 1 and 4; Passeriformes: $p = 0.25$, $R^2 = 0.19$, df: 1 and 7). Additionally, visual examination of the pattern reveals no trend, significant or otherwise (figures. S2-S4). The possible exception is passerines (figure S4), which appear to exhibit a positive relationship between the change in body size with species richness

and body size. This relationship is not statistically significant, however, and there are only 9 genera of sufficient sampling to include in analyses. We caution that the entire body size range for passerines in our dataset is not large: 5.5g (*Tiaris bicolor*) to 54.0g (*Pachycephala pectoralis*). Additionally, the differences in size between the small-bodied passerines which become larger on small islands of low species richness and the large-bodied passerines which become smaller on these islands is not great. The genus *Myzomela* (6.6-17.9g, mean 11.4g) exhibits a significant negative relationship between body size and species richness, while the similarly sized genus *Myiagra* (9.8-24.1g, mean 14.2g) exhibits a significant positive relationship (Table S5). Likewise, the closely related *Coereba flaveola* (mean 9.9g) and *Loxigilla* (mean 20.6g) tanagers change body size on islands in opposite ways (Table S5). Perhaps with more data we might find support for the island rule in passerines. When considered in sum, however, the taxa in our study do not follow the island rule.

Additional Supplemental Figures

Figure S1. Predictions of the island rule. Small-bodied taxa should become larger on islands of lower species richness, and thus exhibit a negative relationship between body size and species richness. Large-bodied taxa should become smaller on islands of low species richness, and thus exhibit a positive relationship between body size and species richness. If most taxa truly are evolving toward an idealized or equilibrium body size, body size changes should be greatest for taxa at the extremes of body size. Some taxa may not change body size consistently on islands, and thus have slopes of 0. These should be primarily medium-sized taxa.

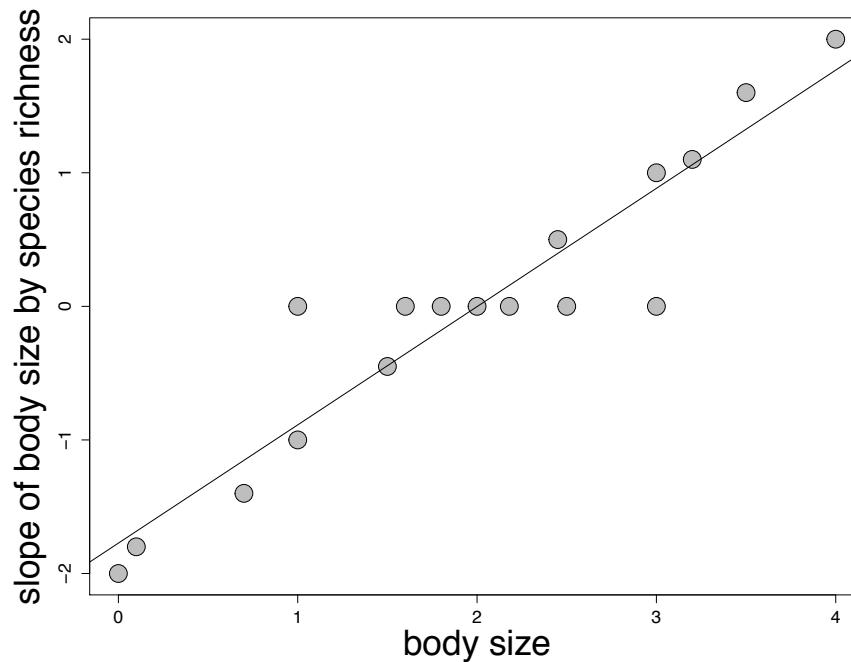


Figure S2. The relationship between body size and island species richness for each genus (y-axis) and mean body size for the genus (x-axis). The size of each point represents the R^2 value for the linear regression model of body size by species richness for that genus. Clade is indicated by color.

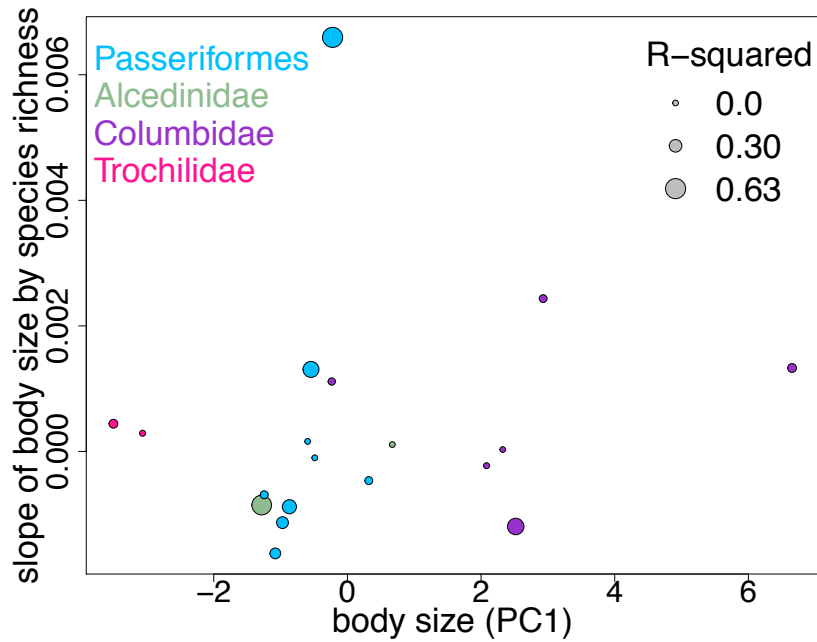


Figure S3. The relationship between body size and island species richness for each genus (y-axis) and mean body size for the genus (x-axis) for Columbidae. The size of each point represents the R^2 value for the linear regression model of body size by species richness for that genus.

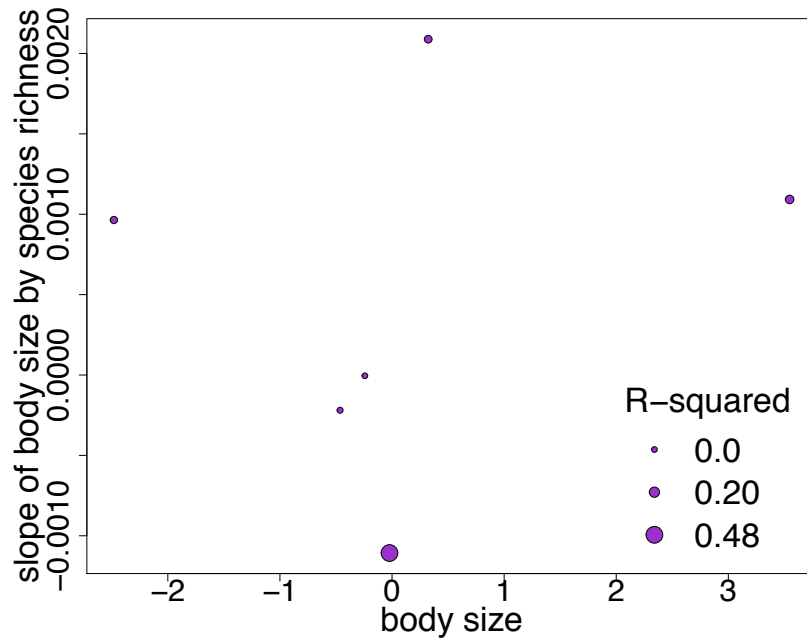
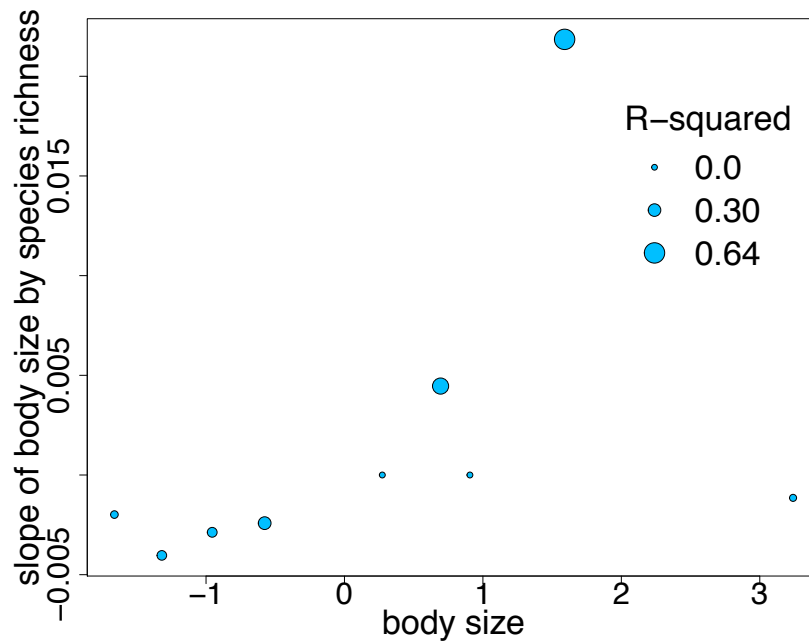


Figure S4. The relationship between body size and island species richness for each genus (y-axis) and mean body size for the genus (x-axis) for Passeriformes. The size of each point represents the R^2 value for the linear regression model of body size by species richness for that genus.



Supplementary Tables

Table S4: Keel and tarsometatarsus lengths are negatively correlated in most taxa. Linear models of body size-corrected keel length predicted by body size-corrected tarsometatarsus length for each focal taxon.

taxon	estimate	p-value	adj. R²	df
<i>Ptilinopus</i>	-3.67	<0.001	0.64	1 and 112
<i>Ducula</i>	-7.32	<0.001	0.49	1 and 60
<i>Columbina</i>	-0.49	0.45	0.0	1 and 73
<i>Macropygia</i>	-4.20	<0.001	0.46	1 and 43
<i>Zenaida aurita</i>	-3.67	<0.001	0.31	1 and 37
<i>Coereba flaveola</i>	-0.62	<0.001	0.34	1 and 237
<i>Loxigilla</i>	-0.91	<0.001	0.22	1 and 195
<i>Tiaris</i>	-0.15	0.32	0.0	1 and 175
<i>Todiramphus</i>	-1.99	<0.001	0.78	1 and 87
Zosteropidae	-0.66	<0.001	0.59	1 and 126
Trochilidae	-6.26	<0.001	0.63	1 and 72
Rhipiduridae	-0.58	<0.001	0.55	1 and 116
Meliphagidae	-0.78	<0.001	0.49	1 and 54
Monarchidae	-0.88	<0.001	0.62	1 and 121
Pachycephalidae	-0.46	<0.001	0.60	1 and 82

Table S5: Results for models predicting the relationship between the air-ground index and island characteristics. Island population means are the units of analysis (analysis 2B).

taxon	predictor	AIC	coefficient	model	adj.	df
	variable(s)			p-value	R²	
all taxa	richness	811.8	0.31	<0.001	0.04	1, 364
all taxa	area	824.7	0.05	0.08	0.01	1, 364
all taxa	richness + family	252.0	0.40	<0.001	0.80	9, 356
all taxa	family	356.9		<0.001	0.73	8, 357
<i>Ptilinopus</i>	richness	31.1	0.68	<0.001	0.56	1, 31
<i>Ptilinopus</i>	area	44.6	0.23	<0.001	0.34	1, 31
<i>Ducula</i>	richness	28.0	0.74	<0.001	0.66	1, 20
<i>Ducula</i>	area	32.7	0.33	<0.001	0.57	1, 20
<i>Columbina</i>	richness	-33.9	0.16	0.17	0.09	1, 11
<i>Columbina</i>	area	-32.5	0.01	0.39	0.0	1, 11
<i>Macropygia</i>	richness	4.8	0.15	0.46	0.0	1, 7
<i>Macropygia</i>	area	5.5	0.02	0.76	0.0	1, 7
<i>Zenaida aurita</i>	richness	1.9	0.19	0.60	0.0	1, 11
<i>Zenaida aurita</i>	area	-0.82	0.11	0.11	0.14	1, 11

taxon	predictor	AIC	coefficient	model	adj.	df
	variable(s)			p-value	R²	
<i>Coereba</i>	richness	-19.4	0.47	0.02	0.20	1, 20
<i>flaveola</i>						
<i>Coereba</i>	area	-18.9	0.08	0.03	0.19	1, 20
<i>flaveola</i>						
<i>Loxigilla</i>	richness	-24.9	-0.09	0.51	0.0	1, 15
<i>Loxigilla</i>	area	-28.4	-0.05	0.06	0.16	1, 15
<i>Tiaris</i>	richness	-61.0	0.22	0.006	0.26	1, 23
<i>Tiaris</i>	area	-56.5	0.03	0.06	0.11	1, 23
<i>Todiramphus</i>	richness	-15.9	0.26	<0.001	0.43	1, 30
<i>Todiramphus</i>	area	-10.3	0.11	<0.001	0.32	1, 30
Zosteropidae	richness	-2.8	0.42	<0.001	0.42	1, 27
Zosteropidae	area	4.6	0.13	0.003	0.26	1, 27
Trochilidae	richness	-23.7	0.09	0.51	0.0	1, 16
Trochilidae	area	-23.7	0.02	0.52	0.0	1, 16
<i>Rhipidura</i>	richness	34.5	0.17	0.20	0.02	1, 33
<i>Rhipidura</i>	area	34.5	0.07	0.20	0.02	1, 33
Meliphagidae	richness	30.7	0.17	0.27	0.01	1, 22
Meliphagidae	area	31.1	0.06	0.36	0.00	1, 22
Monarchidae	richness	8.9	0.28	0.02	0.18	1, 22
Monarchidae	area	11.8	0.09	0.10	0.08	1, 22
<i>Pachycephala</i>	richness	7.3	0.42	0.003	0.32	1, 21

taxon	predictor	AIC	coefficient	model	adj.	df
	variable(s)			p-value	R ²	
<i>Pachycephala</i>	area	14.7	0.10	0.13	0.06	1, 21

Table S6: Results for analyses predicting the relationship between body size and island characteristics. Island population means are the unit of analysis (analysis 2B).

taxon	predictor	AIC	coefficient	model p-	adj. R²	df
	variable(s)			value		
<i>Ptilinopus</i>	richness	80.9	0.023	0.92	0.0	1, 31
<i>Ptilinopus</i>	area	80.9	-0.005	0.96	0.0	1, 31
<i>Ducula</i>	richness	54.1	0.52	0.022	0.20	1, 20
<i>Ducula</i>	area	54.7	0.23	0.030	0.17	1, 20
<i>Columbina</i>	richness	-0.92	0.15	0.71	0.0	1, 11
<i>Columbina</i>	area	-1.77	0.045	0.36	0.0	1, 11
<i>Macropygia</i>	richness	23.2	-0.43	0.43	0.0	1, 7
<i>Macropygia</i>	area	21.6	-0.25	0.18	0.13	1, 7
<i>Zenaida aurita</i>	richness	2.7	0.44	0.26	0.03	1, 11
<i>Zenaida aurita</i>	area	3.1	0.08	0.32	0.0	1, 11
<i>Coereba flaveola</i>	richness	-12.1	-0.24	0.30	0.0	1, 20
<i>Coereba flaveola</i>	area	-12.0	-0.04	0.32	0.0	1, 20
<i>Loxigilla</i>	richness	6.0	1.3	<0.001	0.50	1, 15
<i>Loxigilla</i>	area	4.0	0.29	<0.001	0.56	1, 15
<i>Tiaris</i>	richness	-39.5	-0.16	0.16	0.04	1, 23
<i>Tiaris</i>	area	-37.7	-0.01	0.57	0.0	1, 23
<i>Todiramphus</i>	richness	57.2	0.04	0.82	0.0	1, 30
<i>Todiramphus</i>	area	57.3	-0.01	0.85	0.0	1, 30

taxon	predictor	AIC	coefficient	model p-	adj. R²	df
	variable(s)			value		
Zosteropidae	richness	35.5	-0.20	0.26	0.01	1, 27
Zosteropidae	area	33.9	-0.12	0.09	0.07	1, 27
Trochilidae	richness	8.2	-0.43	0.23	0.03	1, 16
Trochilidae	area	6.9	-0.13	0.11	0.10	1, 16
<i>Rhipidura</i>	richness	67.9	0.02	0.92	0.0	1, 33
<i>Rhipidura</i>	area	67.7	-0.03	0.67	0.0	1, 33
Meliphagidae	richness	64.9	0.29	0.34	0.0	1, 22
Meliphagidae	area	64.8	0.13	0.33	0.0	1, 22
Monarchidae	richness	38.8	-0.17	0.43	0.0	1, 22
Monarchidae	area	39.0	-0.06	0.52	0.0	1, 22
Pachycephalidae	richness	23.9	-0.54	0.007	0.27	1, 21
Pachycephalidae	area	24.7	-0.22	0.010	0.24	1, 21

Table S7: Results for Analysis 3A, predicting shape with island species richness and area. The dependent variable in each model is the air-ground shape variable: the second principal component from a PCA of keel length and tarsometatarsus length. Greater values of the shape variable indicate larger flight muscles and shorter legs. Each data point is one specimen. Island area and species richness values are log-transformed. Models are linear regressions. P-values for each parameter are from ANCOVAs. Unless otherwise noted, area and richness were positively correlated with the shape variable.

taxon	predictor variable(s)	model p- value	adj. R²	p-values for each parameter	df
<i>Ptilinopus</i>	richness	<0.001	0.41		1, 112
<i>Ptilinopus</i>	area	<0.001	0.26		1, 112
<i>Ptilinopus</i>	richness + species + sex	<0.001	0.92	richness <0.001; species <0.001; sex: 0.07	23, 90
<i>Ducula</i>	richness	<0.001	0.43		1, 60
<i>Ducula</i>	area	<0.001	0.38		1, 60
<i>Ducula</i>	richness + species + sex	<0.001	0.60	richness <0.001; species: 0.008; sex: 0.004	13, 48
<i>Columbina</i>	richness	0.25	0.0		1, 73
<i>Columbina</i>	area	0.68	0.0		1, 73

taxon	predictor	model p-	adj.	p-values for each	df
	variable(s)	value	R²	parameter	
<i>Columbina</i>	richness + species + sex	0.03	0.08	richness: 0.23; species: 0.07; sex: 0.03	3, 71
<i>Macropygia</i>	richness	<0.001	0.42		1, 43
<i>Macropygia</i>	area	<0.001	0.30		1, 43
<i>Macropygia</i>	richness + species + sex	<0.001	0.66	richness <0.001; species <0.001; sex: 0.48	5, 39
<i>Zenaida aurita</i>	richness	0.008	0.15		1, 37
<i>Zenaida aurita</i>	area	<0.001	0.27		1, 37
<i>Zenaida aurita</i>	richness + sex	0.01	0.18	richness: 0.007; sex: 0.16	2, 36
<i>Coereba</i> <i>flaveola</i>	richness	<0.001	0.40		1, 237
<i>Coereba</i> <i>flaveola</i>	area	<0.001	0.61		1, 237
<i>Coereba</i> <i>flaveola</i>	richness + sex	<0.001	0.46	richness <0.001; sex <0.001	2, 236
<i>Loxigilla</i>	richness	<0.001	0.08		1, 195
<i>Loxigilla</i>	area	0.08	0.01		1, 195
<i>Loxigilla</i>	richness +	<0.001	0.17	richness <0.001; species	4,

taxon	predictor variable(s)	model p- value	adj. R²	p-values for each parameter	df
	species + sex			<0.001; sex: 0.11	192
<i>Tiaris</i>	richness	<0.001	0.42		1, 175
<i>Tiaris</i>	area	<0.001	0.36		1, 175
<i>Tiaris</i>	richness + species + sex	<0.001	0.53	richness <0.001; species <0.001; sex <0.001	4, 172
<i>Todiramphus</i>	richness	<0.001	0.60		1, 87
<i>Todiramphus</i>	area	<0.001	0.51		1, 87
<i>Todiramphus</i>	richness + species + area	<0.001	0.82	richness <0.001; species <0.001; sex: 0.10	9, 79
Zosteropidae	richness	<0.001	0.23		1, 126
Zosteropidae	area	0.06	0.02		1, 126
Zosteropidae	richness + species + sex	<0.001	0.87	richness <0.001; species <0.001; sex: 0.02	19, 108
Trochilidae	richness	<0.001	0.17		1, 72
Trochilidae	area	<0.001	0.30		1, 72
Trochilidae	richness(-) + species + sex	<0.001	0.77	richness <0.001; species <0.001; sex <0.001	12, 61

taxon	predictor variable(s)	model p- value	adj. R ²	p-values for each parameter	df
Trochilidae	area + species + sex	<0.001	0.77	area <0.001; species <0.001; sex <0.001	12, 61
<i>Rhipidura</i>	richness	0.28	0.00		1, 116
<i>Rhipidura</i>	area	0.77	0.00		1, 116
<i>Rhipidura</i>	richness + species + sex	<0.001	0.90	richness <0.001; species <0.001; sex <0.001	22, 95
Meliphagidae	richness	<0.001	0.42		1, 54
Meliphagidae	area	<0.001	0.38		1, 54
Meliphagidae	richness + species + sex	<0.001	0.83	richness <0.001; species <0.001; sex: 0.001	21, 34
Monarchidae	richness	<0.001	0.28		1, 121
Monarchidae	area	<0.001	0.12		1, 121
Monarchidae	richness + species + sex	<0.001	0.82	richness <0.001; species <0.001; sex <0.001	20, 102
<i>Pachycephala</i>	richness	<0.001	0.25		1, 82
<i>Pachycephala</i>	area	0.05	0.03		1, 82
<i>Pachycephala</i>	richness +	<0.001	0.60	richness <0.001; species	12,

taxon	predictor	model p-	adj.	p-values for each	df
	variable(s)	value	R²	parameter	
	species + sex			<0.001; sex: 0.89	71

Table S8: Results for Analysis 3. Each data point is one specimen. Island area and species richness values are log-transformed. Models are linear regressions. P-values for each parameter are from ANCOVAs. “Keel” and “tarso” are the residuals of regressions of keel length and tarsometatarsus length, respectively, by PC1, to correct for overall body size. Unless otherwise noted, area and richness were positively correlated with keel length and negatively correlated with tarsometatarsus length. The relationship between richness or area and PC1 is indicated by (-) following area/richness for a negative correlation and (+) for a positive correlation.

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
Columbidae						
<i>Ptilinopus</i>	keel	richness	<0.001	0.38		1, 112
<i>Ptilinopus</i>	keel	area	<0.001	0.24		1, 112
<i>Ptilinopus</i>	keel	area + species + sex	<0.001	0.88	area <0.001; species <0.001; sex: 0.3	23, 90
<i>Ptilinopus</i>	keel	richness + species + sex	<0.001	0.88	richness <0.001; species <0.001; sex: 0.3	23, 90
<i>Ptilinopus</i>	tarso	area	<0.001	0.21		1,

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
						112
<i>Ptilinopus</i>	tarso	richness	<0.001	0.34		1, 112
<i>Ptilinopus</i>	tarso	area + species + sex	<0.001	0.92	area: 0.99; species <0.001; sex: 0.4	23, 90
<i>Ptilinopus</i>	tarso	richness + species + sex	<0.001	0.92	richness: 0.97; species <0.001; sex: 0.4	23, 90
<i>Ptilinopus</i>	PC1	area(-)	0.40	0.00		1, 112
<i>Ptilinopus</i>	PC1	richness(-)	0.41	0.00		1, 112
<i>Ptilinopus</i>	PC1	area(-) + species + sex	<0.001	0.92	area: 0.004; species <0.001; sex <0.001	23, 90
<i>Ptilinopus</i>	PC1	richness(-) + species + sex	<0.001	0.92	richness: 0.005; species <0.001; sex <0.001	23, 90
<i>Ducula</i>	keel	richness	<0.001	0.60		1, 60

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
<i>Ducula</i>	keel	area	<0.001	0.53		1, 60
<i>Ducula</i>	keel	richness + species + sex	<0.001	0.74	richness: 0.42; species <0.001; sex: 0.02	13, 48
<i>Ducula</i>	keel	area + species + sex	<0.001	0.74	area: 0.93; species <0.001; sex: 0.02	13, 48
<i>Ducula</i>	tarso	richness	<0.001	0.32		1, 60
<i>Ducula</i>	tarso	area	<0.001	0.27		1, 60
<i>Ducula</i>	tarso	richness + species + sex	<0.001	0.60	richness: 0.65; species <0.001; sex: 0.02	13, 48
<i>Ducula</i>	PC1	area(+)	<0.001	0.20		1, 60
<i>Ducula</i>	PC1	richness(+)	<0.001	0.24		1, 60
<i>Ducula</i>	PC1	richness(-) + species + sex	<0.001	0.79	richness <0.001; species <0.001;	13, 48

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
					sex: 0.002	
<i>Columbina</i>	keel	richness	0.16	0.01		1, 73
<i>Columbina</i>	keel	area	0.06	0.03		1, 73
<i>Columbina</i>	keel	richness + species + sex	0.02	0.09	richness: 0.43; species: 0.01; sex: 0.1	3, 71
<i>Columbina</i>	keel	area + species + sex	0.009	0.11	area: 0.13; species: 0.009; sex: 0.09	3, 71
<i>Columbina</i>	tarso	richness	0.27	0.00		1, 73
<i>Columbina</i>	tarso	area	0.35	0.00		1, 73
<i>Columbina</i>	tarso	richness + species + sex	0.02	0.09	richness: 0.06; species: 0.02; sex: 0.29	3, 71
<i>Columbina</i>	PC1	area(+)	0.01	0.07		1, 73
<i>Columbina</i>	PC1	richness(+)	0.04	0.05		1,

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
						73
<i>Columbina</i>	PC1	richness(+) + species + sex	<0.001	0.46	richness <0.001; species <0.001; sex: 0.03	3, 71
<i>Macropygia</i>	keel	richness	<0.001	0.37		1, 43
<i>Macropygia</i>	keel	area	<0.001	0.22		1, 43
<i>Macropygia</i>	keel	richness(-) + species + sex	<0.001	0.64	richness: 0.84; species <0.001; sex: 0.51	5, 39
<i>Macropygia</i>	tarso	richness	<0.001	0.34		1, 43
<i>Macropygia</i>	tarso	area	<0.001	0.25		1, 43
<i>Macropygia</i>	tarso	richness + species + sex	<0.001	0.52	richness: 0.13; species <0.001; sex: 0.11	5, 39
<i>Macropygia</i>	PC1	richness(-)	0.86	0.00		1, 43
<i>Macropygia</i>	PC1	area(-)	0.26	0.01		1,

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
						43
<i>Macropygia</i>	PC1	richness(-) + species + sex	<0.001	0.81	richness: 0.77; species <0.001; sex: 0.009	5, 39
<i>Zenaida aurita</i>	keel	richness	<0.001	0.28		1, 37
<i>Zenaida aurita</i>	keel	area	<0.001	0.41		1, 37
<i>Zenaida aurita</i>	keel	richness + sex	0.001	0.27	richness <0.001; sex: 0.43	2, 36
<i>Zenaida aurita</i>	tarso	richness	0.15	0.03		1, 37
<i>Zenaida aurita</i>	tarso	area	0.03	0.10		1, 37
<i>Zenaida aurita</i>	tarso	richness + sex	0.25	0.02	richness: 0.15; sex: 0.42	2, 36
<i>Zenaida aurita</i>	PC1	richness(+)	0.04	0.08		1, 37
<i>Zenaida aurita</i>	PC1	area(+)	0.04	0.09		1, 37
<i>Zenaida aurita</i>	PC1	richness(+) +	<0.001	0.33	richness: 0.02;	2,

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
		sex			sex <0.001	36
Thraupidae						
<i>Coereba flaveola</i>	keel	richness	<0.001	0.21		1, 237
<i>Coereba flaveola</i>	keel	area	<0.001	0.38		1, 237
<i>Coereba flaveola</i>	keel	richness + sex	<0.001	0.37	richness <0.001; sex <0.001	2, 236
<i>Coereba flaveola</i>	keel	area + sex	<0.001	0.52	area <0.001; sex <0.001	2, 236
<i>Coereba flaveola</i>	tarso	richness	<0.001	0.31		1, 237
<i>Coereba flaveola</i>	tarso	area	<0.001	0.38		1, 237
<i>Coereba flaveola</i>	tarso	richness + sex	<0.001	0.39	richness <0.001; sex: 0.06	2, 236
<i>Coereba flaveola</i>	tarso	area + sex	<0.001	0.46	area <0.001; sex: 0.004	2, 236
<i>Coereba flaveola</i>	PC1	richness(-)	<0.001	0.13		1, 237
<i>Coereba flaveola</i>	PC1	area(-)	<0.001	0.18		1,

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
						237
<i>Coereba flaveola</i>	PC1	richness(-) + sex	<0.001	0.37	richness <0.001; sex <0.001	2, 236
<i>Loxigilla</i>	keel	richness	<0.001	0.12		1, 195
<i>Loxigilla</i>	keel	area	<0.001	0.08		1, 195
<i>Loxigilla</i>	keel	richness + species + sex	<0.001	0.32	richness <0.001; species <0.001; sex: 0.18	4, 192
<i>Loxigilla</i>	tarso	richness	0.02	0.02		1, 195
<i>Loxigilla</i>	tarso	area	0.24	0.00		1, 195
<i>Loxigilla</i>	tarso	richness + species + sex	<0.001	0.12	richness <0.001; species <0.001; sex: 0.14	4, 192
<i>Loxigilla</i>	PC1	richness(+)	<0.001	0.62		1, 195
<i>Loxigilla</i>	PC1	area(+)	<0.001	0.56		1, 195

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
<i>Loxigilla</i>	PC1	richness(+) + species + sex	<0.001	0.87	richness <0.001; sex <0.001; species <0.001	4, 192
<i>Tiaris</i>	keel	richness	<0.001	0.25		1, 175
<i>Tiaris</i>	keel	area	<0.001	0.23		1, 175
<i>Tiaris</i>	keel	richness + species + sex	<0.001	0.40	richness <0.001; species: 0.003; sex <0.001	4, 172
<i>Tiaris</i>	tarso	richness	<0.001	0.12		1, 175
<i>Tiaris</i>	tarso	area	<0.001	0.10		1, 175
<i>Tiaris</i>	tarso	richness + species + sex	<0.001	0.28	richness <0.001; species <0.001; sex: 0.73	4, 172
<i>Tiaris</i>	PC1	richness(-)	<0.001	0.07		1, 175
<i>Tiaris</i>	PC1	area(-)	0.009	0.03		1, 175

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
<i>Tiaris</i>	PC1	richness(+) + species + sex	<0.001	0.37	richness <0.001; species <0.001; sex: 0.01	4, 172
Alcedinidae						
<i>Todiramphus</i>	keel	richness	<0.001	0.56		1, 87
<i>Todiramphus</i>	keel	area	<0.001	0.46		1, 87
<i>Todiramphus</i>	keel	richness + species + sex	<0.001	0.72	richness <0.001; species <0.001; sex: 0.32	9, 79
<i>Todiramphus</i>	tarso	richness	<0.001	0.62		1, 87
<i>Todiramphus</i>	tarso	area	<0.001	0.52		1, 87
<i>Todiramphus</i>	tarso	richness + sex + species	<0.001	0.87	richness <0.001; species <0.001; sex: 0.03	9, 79
<i>Todiramphus</i>	PC1	richness(+)	0.18	0.00		1, 87
<i>Todiramphus</i>	PC1	area(+)	0.54	0.00		1,

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
						87
<i>Todiramphus</i>	PC1	richness(-) + species + sex	<0.001	0.83	richness: 0.001; species <0.001; sex: 0.71	9, 79
Zosteropidae	keel	richness	<0.001	0.11		1, 126
Zosteropidae	keel	area	0.29	0.00		1, 126
Zosteropidae	keel	richness + species + sex	<0.001	0.74	richness <0.001; species <0.001; sex: 0.06	19, 108
Zosteropidae	tarso	richness	<0.001	0.30		1, 126
Zosteropidae	tarso	area	0.03	0.03		1, 126
Zosteropidae	tarso	richness + species + sex	<0.001	0.91	richness <0.001; species <0.001; sex: 0.01	19, 108
Zosteropidae	PC1	richness(-)	0.02	0.03		1, 126
Zosteropidae	PC1	area(-)	0.03	0.03		1,

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
						126
Zosteropidae	PC1	richness(-) + species + sex	<0.001	0.94	richness <0.001; species <0.001; sex: 0.22	19, 108
Trochilidae	keel	richness	<0.001	0.14		1, 72
Trochilidae	keel	area	<0.001	0.23		1, 72
Trochilidae	keel	richness(-) + species + sex	<0.001	0.78	richness <0.001; species <0.001 sex <0.001;	12, 61
Trochilidae	keel	area + species + sex	<0.001	0.79	area <0.001; species <0.001; sex <0.001	12, 61
Trochilidae	tarso	richness	0.01	0.07		1, 72
Trochilidae	tarso	area	<0.001	0.21		1, 72
Trochilidae	tarso	richness(+) + species + sex	<0.001	0.57	richness <0.001; species <0.001; sex: 0.01	12, 61

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
Trochilidae	tarso	area + species + sex	<0.001	0.58	area <0.001; species <0.001; sex: 0.01	12, 61
Trochilidae	PC1	richness(-)	<0.001	0.17		1, 72
Trochilidae	PC1	area(-)	<0.001	0.14		1, 72
Trochilidae	PC1	richness(+) + species + sex	<0.001	0.95	richness <0.001; species <0.001; sex <0.001	12, 61
Rhipiduridae						
<i>Rhipidura</i>	keel	richness(-)	0.19	0.01		1, 116
<i>Rhipidura</i>	keel	area(-)	0.11	0.01		1, 116
<i>Rhipidura</i>	keel	richness(-) + species + sex	<0.001	0.80	richness: 0.004; species <0.001; sex <0.001	22, 95
<i>Rhipidura</i>	keel	area(+) + species + sex	<0.001	0.80	area <0.001; species <0.001; sex <0.001	22, 95

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
<i>Rhipidura</i>	tarso	richness	0.004	0.06		1, 116
<i>Rhipidura</i>	tarso	area	0.06	0.02		1, 116
<i>Rhipidura</i>	tarso	richness + species + sex	<0.001	0.93	richness <0.001; species <0.001; sex <0.001	22, 95
<i>Rhipidura</i>	PC1	richness(+)	0.10	0.01		1, 116
<i>Rhipidura</i>	PC1	area(-)	0.89	0.00		1, 116
<i>Rhipidura</i>	PC1	richness(+) + species + sex	<0.001	0.91	richness <0.001; species <0.001; sex 0.003	22, 95
Meliphagidae	keel	richness	<0.001	0.24		1, 54
Meliphagidae	keel	area	<0.001	0.22		1, 54
Meliphagidae	keel	richness + species + sex	<0.001	0.84	richness <0.001; species <0.001; sex <0.001	21, 34

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
Meliphagidae	tarso	richness	<0.001	0.52		1, 54
Meliphagidae	tarso	area	<0.001	0.47		1, 54
Meliphagidae	tarso	richness + sex + species	<0.001	0.73	richness <0.001; species: 0.008; sex <0.001	21, 34
Meliphagidae	PC1	richness(+)	0.73	0.0		1, 54
Meliphagidae	PC1	area(-)	0.71	0.0		1, 54
Meliphagidae	PC1	richness(-) + species + sex	<0.001	0.92	richness: 0.22; species <0.001; sex: 0.006	21, 34
Monarchidae	keel	richness	<0.001	0.24		1, 121
Monarchidae	keel	area	<0.001	0.14		1, 121
Monarchidae	keel	richness(-) + species + sex	<0.001	0.81	richness <0.001; sex <0.001; species <0.001	20, 102

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
Monarchidae	tarso	richness	<0.001	0.22		1, 121
Monarchidae	tarso	area	0.001	0.09		1, 121
Monarchidae	tarso	richness(+) + species + sex	<0.001	0.88	richness <0.001; species <0.001; sex: 0.03	20, 102
Monarchidae	PC1	richness(-)	0.22	0.00		1, 121
Monarchidae	PC1	area(-)	0.15	0.01		1, 121
Monarchidae	PC1	richness(+)+ species + sex	<0.001	0.89	richness <0.001; species <0.001; sex <0.001;]	20, 102
Pachycephalidae						
<i>Pachycephala</i>	keel	richness	<0.001	0.20		1, 82
<i>Pachycephala</i>	keel	area	0.01	0.06		1, 82
<i>Pachycephala</i>	keel	richness + species + sex	<0.001	0.32	richness <0.001; species: 0.01; sex:	12, 71

taxon	model	predictor variable(s)	model p-value	adj. R ²	p-values for each parameter	df
					0.18	
<i>Pachycephala</i>	tarso	richness	<0.001	0.37		1, 82
<i>Pachycephala</i>	tarso	area	0.001	0.12		1, 82
<i>Pachycephala</i>	tarso	richness + species + sex	<0.001	0.82	richness <0.001; species <0.001; sex: 0.03	12, 71
<i>Pachycephala</i>	PC1	richness(-)	0.19	0.01		1, 82
<i>Pachycephala</i>	PC1	area(-)	0.002	0.10		1, 82
<i>Pachycephala</i>	PC1	richness(-) + species + sex	<0.001	0.36	richness: 0.11; species <0.001; sex: 0.58	12, 71
<i>Pachycephala</i>	PC1	area(-) + species + sex	<0.001	0.41	area <0.001; species <0.001; sex: 0.46	12, 71

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